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TABLE OF CONTENTS

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7301

Item 17 - Data Collection and Analytical Needs, presented by Norman Abramson.

Before discussing data and analysis needs, we must determine why data and analysis are required. At all costs we must avoid the collection of data just for the sake of accumulating it, and then deciding what it is good for at some later time. All too often we fisheries workers have collected data without having a well defined plan for its utilization.

In general, we may state that data are needed in order to manage the fisheries. However, that answer is too simple to guide the design of data collection and management research programs as we wish to do at this workshop. To help delineate the objectives more clearly, I have chosen to divide management arbitrarily into the following three levels of sophistication.

Level 1. Based upon a general knowledge of the abundance of stocks of interens, be able to detect problems so that concentrated programs can be directed at these areas. This is probably the minimum level of management that most firheries administrators would wish to employ.

Level 2. To control stock size, stock productivity, and catch by means of regulatory activities. This type of management is usually aimed at obtaining the maximum yield in weight from a stock, consistent with conservation of the resource.

Level 3. This highest level of sophistication in management schemes would aim at optimizing the use of the resource in terms of economic or social benefits. The level of harvesting and the distribution of the catch among the fishing units would, in general, not coincide with those determined under Level 2 Management.

It should be pointed out that Level 2 Management has rarely been achieved in proctice and the much more complicated Level 3 schemes remain in the discussion stage. Of course, most of our fisheries are regulated using regulatory devices which would be appropriate to Level 2 or Level 3 management, but the regulations are not generally based upon the information required to attain true management.

When we consider the types of data which are needed and the analytical methods to be employed for attaining a particular management level, it will be necessary to classify each fishery according to its particular characteristic. These fishery characteristics determine, to some extent, the types of regulatory mechanisms which can successfully be employed and thus are relevant when designing data collection and analytical plans. The fishery characteristics I refer to are: primarily recreational, primarily commercial, both recreational and commercial, single species fishery, or multi-species fishery. It will be seen that the list of species on the agenda of this Workshop includes representatives which can be assigned to each of these categories.

Data or Estimates Needed for Level 1 Management

Level 1 Management of a single species fishery ordinarily can be carried out if relative abundance of the stock is known. Traditionally, relative abundance has been estimated with the use of catch-per-unit-effort statistics. The implicit assumption involved in such use of catch-per-effort is that however the statistic is calculated, it will be proportional to the abundance of the stock. To be meaningful the effort units must be standardized in a way that corrects for changes in efficiency as a function of time and the effects of aggregation of the fishing units on the fish. In addition, unless a constant fraction of the stock is always available to fishery, compensation must be made for changes in availability over time. Many anomalies which appear when observing catch-per-unit-effort statistics are probably due to such uncompensated changes in availability.

For Level 1 management of multi-species fishery, all of the above information will be needed. In addition, an additional effort adjustment will be required for preferred species effects. Without such an adjustment, raw effort statistics will tend to be overestimates relative to those species which are only secondarily sought after.

Data or Estimates Needed for Level 2 Management

Level 2 management, aimed at maximizing the sustainable yield, usually will utilize one of two types of yield models-a Surplus Production Model or a Dynamic Pool Model.

Management based upon a Surplus Production or Schaefer-type Model is generally unsuitable for recreational fisheries. Since regulation is carried out by setting a quota on the aggregate amount of catch or effort. There would be great technical as well as public relations problems in conducting this type of regulation on a sport fishery. Because of this, and because of assumptions associated with these models, they are most useful for commercial fisheries which exploit short-lived species. Also, they may offer the most feasible management methods for unageable animals.

Employment of this method on a single-species commercial fishery, requires statistics giving catch in weight, effort standardized for efficiency, and the distribution of fishing effort relative to the exploited population. Since existent fitting methods perform rather poorly at estimating the catchability coefficient and the population size, it is highly desirable to have independent estimates of one of these parameters. For example, independent population estimates might be obtained from egg and larval surveys, from a combination of mortality rate estimates and numbers of fish in the landings, or from direct sea survey estimates of biomass. With the surplus production model it is especially important that catch-per-unit-effort can be assumed proportional to the average population size over the time interval utilized.

To use a Surplus Production Model on one species taken by a multi-species fishery requires, in addition to the factors mentioned above, an correct adjustment is difficult to determine.

Management based on a dynamic pool model may involve either the yield-per-recruit form or a model of the full system. The latter would incorporate a density dependent recruit-spawner relationship and possibly density dependent growth and mortality rates. Estimates of the density dependent effects are so elusive that the yield-per-recruit model has generally been used in management. It has been used to promulgate management regulations for several California recreational species.

Estimates of the following population parameters are requisites for using a dynamic pool model in any fishery situation.

A growth in weight function is required. The data needed to develop this function may be obtained from measuring, weighing, and aging the animals. Alternatively, such a function can be developed from data obtained by growth over a time interval, as determined from tagging experiments.

The natural mortality rate is also needed. This is probably the most difficult parameter to estimate and consequently it is missing from most data sets which otherwise could be used to fit the yield-per-recruit model.

If both total and fishing mortality rate estimates are available, natural mortality may be estimated by subtraction. It can also be obtained from series consisting of total mortality estimates and effort statistics which apply to identical time periods. Here it is essential that fishing mortality can be assumed proportional to effort.

If the species being investigated is taken by a fishery regulated under a size limit, natural mortality may be estimated from the decline in abundance of a year class during the pre-size limit ages. It can also be estimated from the decline in abundance of a year class during the closed season from either statistics gathered from the fishery or from research vessel estimates of abundance. The preceding methods require the assumption that natural mortality does not change with age, in the first case, and that natural mortality does not exhibit seasonal systematic changes, in the second case.

Rough estimates of the natural mortality rate can be deduced from von Bertalanffy growth curve parameters. Estimates of M from this source are not sufficiently accurate for analytical purposes.

Another needed component of the dynamic pool model is the fishing mortality rate. Many methods exist for estimating F, mostly involving the use of tagging experiments.

It can also be estimated from the catch in numbers over a time period and the average total population over the same period. For example, total population might be determined from an egg and larval survey.

F also could be estimated from effort statistics if it is assumed that fishing mortality is proportional to effort and if the relationship between effort and F has been established. The Murphy Method is useful for obtaining a time series of fishing mortality estimates, but it requires that natural mortality be known and that an independent estimate of F be available for a single time interval within the series.

In addition to the preceding parameter estimates required for the yield-per-recruit model, a function relating recruitment to spawning stock is needed for a full self generating dynamic pool model. Based upon data and examples that have appeared on the literature, this function is very difficult to determine. The difficulty may stem from the fact that the assumed mathematical models which have been used are not actually descriptive of the relationship, or because the statistics used to fit the model have very high variability. Since the fitting procedure involves a regression, and only one observation is available for each year, a sufficiently large number of data points has rarely, if ever, been available. Data sources for fitting such models include aged data and accompanying effort statistics or Murphy Method estimates of the absolute abundances of a series of year classes. Other more direct methods of estimating year class abundances might also be used.

I should be pointed out that one of the difficulties in using a dynamic pool model for management purposes, particularly the case of setting a size limit based on a yield-per-recruit model, is that each possible optimum size limit accompanies a different fishing mortality. To regulate a sport fishery by means of a fixed size limit, control over the amount of fishing effort would be needed for optimum management. Alternatively, fishing effort could be continuously measured and the size limit adjusted accordingly.

Data or Estimates Needed for Level 3 Management

Before data collection can be planned for Level 3 management, administrative decisions must be reached which define the regions over which optimization will be attempted. Such regions for potential optimization could range from the maximum satisfaction of the aggregate of anglers to the maximum economic contribution to a geographic area. For a mixture of sport and commercial fisheries utilizing the same species, more that one region for optimization may be selected and some formula devised for allocating the resource among competing users. Even for pure recreational fishery, economic aspects as well as angler satisfaction are involved.

Level 3 management of single-or multi-species recreational fishery, requires all of the data base needed for Level 2 management. Assuming some type of angler satisfaction optimization were chosen as a criterion, a great deal of data should be collected regarding the constitution of individual angler's bags. These data should include the numbers of fish composing the bags, the sizes of the fish, the species composition, and the catch rate. Since we have virtually no objective information on the factors which give satiffaction to the sport fisherman, some type of psychological or sociological study should be mounted to measure the satisfaction effects of the aforementioned factors. In addition, such things as the relation of satisfaction to the individual's catch relative to bag or size limits should be evaluated. I believe that as we face increasing angling pressure and substantially nonincreasing fish stocks, we will have to investigate the various factors that give people pleasure from recreational fishing.

With regard to measuring economic benefits resulting from sport fishing activities, data are required on expenditures made for fares and admissions, bait and tackle, and other angling related expenses. Other quantities of possible value include the worth of sport caught fish on a market basis, benefits to businesses only indirectly related to angling, and perhaps the replacement value of the fishing experience. The latter refers to what an angler would charge to give up his right to engage in recreational fishing.

Species or species groups of interest primarily to the commercial fishing industry might be managed at Level 3 based on certain economic measures. These might include net income to the fishery aggregate, income to boat owners, income to fishermen, income to processors, and income to processing workers. A fishery's contribution to the regional economy may well also be a measure of interest.

It is possible that even in a commercial fishery some measure of occupational satisfaction will warrant consideration when promulgating management regulations. For example, many commercial fishermen could earn a greater income in shoreside occupations but prefer the way of life involved in fishing. In a sense, the fisherman is always gambling that he will make a "big strike" which may also be part of the allure attached to this occupation.

Experimental Management

During the preceding discussions of management under the several levels of sophistication, we have assumed, at least in the case of Levels 2 and 3, that analytical mathematical models would be used to describe the fishery and its effects. Data collection would be designed to estimate parameters and thus fit the models to the data. With sufficiently flexible regulatory mechanisms, management could be conducted on an experimental basis by observing the effects of various types of regulations. However, some type of measurement both of the stocks and of social and economic benefits would be required in order to evaluate the results of experimental management efforts. Perhaps, in view of the difficulties which have been encountered in developing and fitting relaistic mathematical models to fish populations, this experimental approach might be the most realistic and fruitful method of engaging in fisheries management.

Environmantal Conditions

Environmental measurements have not been discussed in the foregoing paragraphs. To the extent that availability is a function of the environment, and there appears to be a strong relationship for many of the subject species, the ability to predict environmental conditions in turnavailability would be a powerful management tool. Availability is, or can be, a component of all models and management methods; consequently predictions of availability may be incorporated into the management schemes.

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7302

R. A. Barkley

The Kuroshio current

The Kuroshio is one of the world's major ocean currents, equal in volume to some 6000 large rivers. Its sudden variations can have disastrous effects on Japanese fisheries, but as oceanographers develop routine monitoring methods fish catches could increase threefold

EVERY second the Kuroshio current carries some 50 million tonnes of sea water past Japan's southeast coast—a flow equal in volume to about 6000 rivers the size of the Danube or Volga. But even this massive current would take some 250 years to equal the total volume of the north Pacific. Thus, although the Kuroshio is one of the major currents in the world's oceans, and plays a vital role in the circulation of the north Pacific, it occupies only a small fraction (less than 0.1 per cent) of that ocean: a thin narrow band less than 100km in width and about 1km at maximum depth running for 3000km along the western edge of the Pacific between the Philippines and the east coast of Japan.

Asia's seamen have known the Kuroshio since ancient times. They named it Kuro-shio (which means 'black stream' in the Japanese language) because of the deep ultramarine colour of the warm, high salinity water which is found flowing north on the right hand side (looking downstream) of the current's axis. The heat which is carried north by this flow influences the weather throughout the northern hemisphere. The Kuroshio therefore plays an indirect but important part in the everyday life of the fishermen and farmers of eastern Asia and also, to a lesser extent, in the lives of most of the rest of mankind as well.

The first European chart to show the Kuroshio was Varenius' "Geographia Generalis" of 1650. Later, expeditions headed by Captains James Cook (1776-80) and Krusenstern (1804) added to western knowledge about the Kuroshio. Although Japanese scientists began to study the biology of the Kuroshio in 1880, it was not until 1893, when Wade started a series of drift bottle experiments, that systematic examination of its currents first began.

Today, in an attempt to learn more about the Kuroshio, scientists from China, Indonesia, Japan, Korea, Philippines, Singapore, Thailand, Hong Kong, United States, the Soviet Union and Vietnam are engaged in a major international project called the Co-operative Study of the Kuroshio (CSK). By keeping a figurative finger on this pulse of the north Pacific, they hope to learn more about western boundary currents in general, the Kuroshio in particular, and the whole north Pacific Ocean as well. In the process, they should also learn more about the way in which both weather and climate respond to changes in conditions at sea, and the ways in which marine animals and plants are affected by their environment.

THE INFLUENCE exerted on ocean currents by the Earth's rotation was not generally appreciated until 1835, when G. de Coriolis, while studying equations of motion in a rotating frame of reference, discovered what is now called coriolis force. Coriolis showed how the effects of the Earth's rotation could be incorporated into the Newtonian equations of motion by adding two additional terms. One, the centrifugal force of the Earth's rotation, is usually absorbed into a redefined term for 'gravitation', which includes gravity and centrifugal forces together and acts along a vertical defined by the direction of a plumb bob. By this definition there is no horizontal component of either force. The other term, the coriolis force, makes

PATH OF THE KUROSHIO is shown in heavy shading on this streamline chart prepared from geostrophic current measurements. The region of narrow intense flow east of Japan is the Kuroshio extension, which differs from the Kuroshio in that it has no land boundary to generate frictional flow. Convergence and divergence is shown by streamlines terminating and beginning

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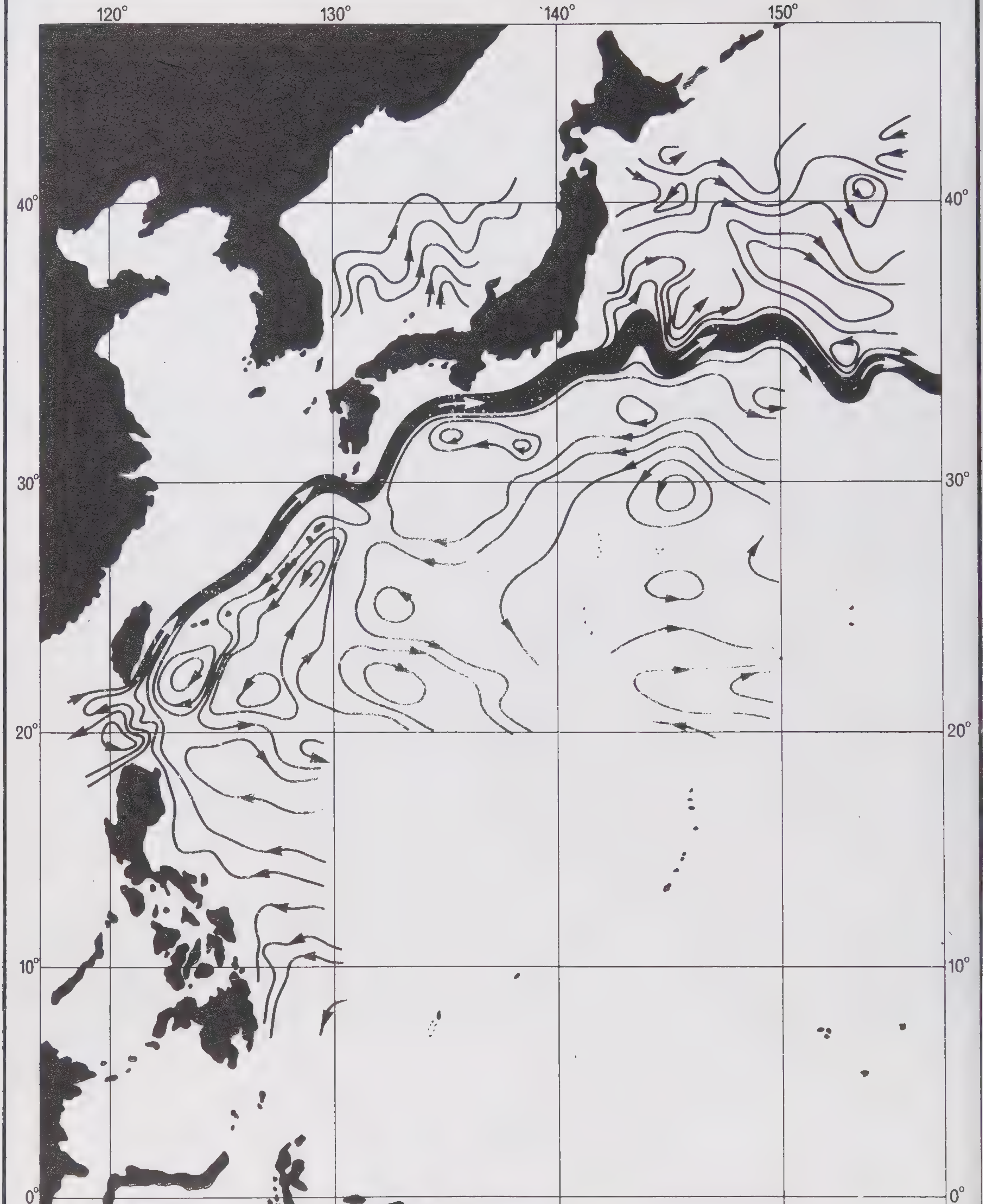
Dr Richard Andrew Barkley is Research Oceanographer at the Bureau of Commercial Fisheries Biological Laboratory in Honolulu. He has worked on the hydrodynamics of the Kuroshio-Oyashio front and his present research is concerned with distribution of temperature, salinity and oxygen in the Pacific Ocean, and with the currents and mixing which control these distributions.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allowance for the effects of conservation of angular momentum on a particle which moves relative to the Earth's surface. Coriolis force acts at right angles to such motion and also at right angles to the Earth's axis of rotation, and thus has no effect on the energy of motion but only modifies its direction.

The vertical component of coriolis force is so small when compared to the force of gravitation that it can always be neglected in ocean current theory. In the sea, however, forces which act along the horizontal are generally weak. Indeed, frictional and inertial forces are far smaller than those we are accustomed to on land—by at least five orders of magnitude—and they have little or no effect on any but the fastest moving ocean currents. The forces exerted by wind stress are often even weaker. Thus the horizontal component of the weak coriolis force becomes an important factor when considering ocean currents.

In most ocean currents the horizontal pressure gradient is found to be in balance with coriolis force. Such currents are called geostrophic or 'Earth-balanced' currents. Thus it is possible to obtain a useful approximation (to within 15 per cent) to actual currents by making measurements of horizontal pressure gradients. To do this, a series of temperature and salinity measurements is made to depths of 1km or more at several locations (called 'stations') across a current. These observations define the field of density (which depends on temperature, salinity and pressure, or depth), from which horizontal pressure gradients can be computed. A chart showing this field of pressure gradients is equivalent to a chart showing streamlines of geostrophic flow. This procedure is referred to as the dynamic method, and was first used by J. W. Sandstrom and B. Helland-Hansen in 1903. Unlike direct current measurements, which are more expensive and time consuming to make and more difficult to interpret, the dynamic method is little affected by transient motion due to surface waves, tides and winds, which are often much stronger than the movements of water in the permanent current system.

Geostrophic current calculations have one major drawback—they only give information on the flow relative to some reference surface which is presumed to be nearly motionless. The problem arises because the dynamic method depends upon an integration, and the constant of integration—the absolute pressure at some level surface common to all the oceanographic stations used in the calculations—is not normally known, and cannot be measured directly with the required accuracy. In practice it is common to use the 1000 decibar surface (at very nearly 1000 metres depth) as a reference surface for measurements used in dynamic calculations.

The theory of wind driven ocean currents concerns itself primarily with the forces which generate, control and finally dissipate energy in the sea. Most of this energy appears in two forms: kinetic energy of motion—the currents *per se*—and potential energy of position—the 'pressure head' due to slopes in the sea's surface and the internal density structure. There are also others, primarily thermal energy, which affect the distribution of density and thereby influence currents.

Those forces which carried Kuroshio water through nets set by Japanese fishermen this morning were generated weeks, months, or even years earlier by winds blowing over the entire north Pacific Ocean. Even a small gust of wind rippling the quiet waters off Baja, California, for example, contributes to the oceanwide accumulation of energy which drives the inexorable flow of millions of tonnes of water past Asia's coasts. A major problem in ocean theory is to determine the way in which energy is transferred from the winds to the shallow wind driven upper layers of the ocean; from there, into the geostrophic currents; and, finally, into the narrow sheer zone on the left hand side of the Kuroshio, where energy is dissipated.

When V. W. Ekman provided, in 1905, a theoretical explanation for Nansen's observation that Arctic icebergs tend to drift to the right of the wind, he laid a major cornerstone for all subsequent studies of wind driven flow. Ekman showed that a steady wind produces transport of water at right angles to the wind's direction (toward the right in the northern hemisphere, and to the left in the southern hemisphere). This movement of water is usually called Ekman transport. A balance is reached between coriolis force and wind stress at the sea surface, which is a precise analogy to the balance existing between coriolis force and the horizontal pressure gradient in geostrophic flow.

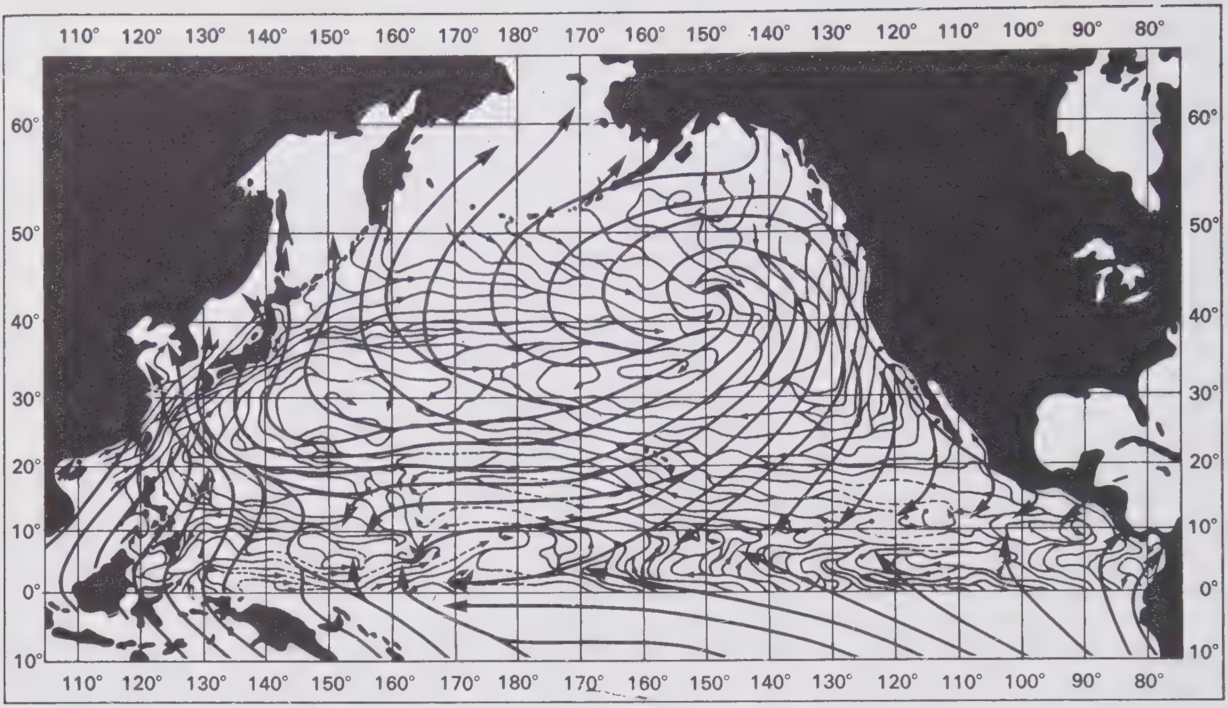
In 1947, H. U. Sverdrup, the Norwegian oceanographer and meteorologist, used Ekman's concepts to calculate the wind driven transport in equatorial currents of the Pacific Ocean. The following year H. Stommel showed that changes in the coriolis effect with latitude (the horizontal component of coriolis force varies as the sine of the latitude, so that it reaches a maximum value at the pole, and vanishes at the equator), were responsible for the narrow swift currents along the western boundaries.

A major advance in the theory of wind driven circulation was made by W. H. Munk in his pioneer study of oceanwide transports. He pointed out the fundamental importance of wind sheer, or torque, which transmits angular momentum to the sea surface and thus generates the major circulation systems. Munk's study was based on a linear steady state mathematical model in which friction played a large part. K. Hidaka has explored such theoretical models extensively since 1949.

In more recent years the importance of large scale friction in currents such as the Kuroshio and Gulf Stream has been questioned by a number of theoreticians, who regard it as characteristic of the climatic-mean flow, but not of the instantaneous current. That is, meanders and eddies formed from time to time by the current could be considered as a form of turbulent friction of the magnitude required in Munk's and Hidaka's theories, if their effects were averaged over large areas over long periods of time. On a shorter time scale, and over smaller distances, such meanders and eddies must be treated individually, which requires the use of nonlinear time dependent mathematical models. Such models present formidable mathematical difficulties which in some cases can only be overcome by the use of numerical computer methods.

PREVAILING SURFACE WINDS over the north Pacific in summer describe a clockwise circulation around the mid-latitude high pressure cell, from which the air spirals outward, away from the high, towards the low pressure regions over Asia and Alaska, and towards the climatic Equator, the doldrums, near 5°N. Initially, this is cool, dry air which descends towards the sea surface and speeds up, removing both heat and moisture from the surface water layers as it goes. It then slows down as it reaches the convergent lows, where the air rises and much of the moisture returns to the sea as rain. In winter, the high pressure band moves south some 20° of latitude and splits into eastern and western cells, with a low pressure band, the Aleutian low, all across the Pacific farther north.

On streamline charts (such as the map on page 55), constant amounts of water flow between any two streamlines (within the accuracy of the methods used), so velocity of flow is inversely proportional to the distance between adjacent streamlines. In addition, such charts show convergences and divergences, flow of water downward out of the layer in question, or upward from below, by showing streamlines terminating (convergence) or beginning



EKMAN TRANSPORT in the north Pacific is shown in the map above, where the prevailing winds in July are shown in colour, and the surface current streamlines in black. Off the coast of California, and the northeast coasts of China and Japan, the wind blows along the coast, inducing offshore transport of water. The opposite situation, where Ekman transport carries surface water towards the coast can be seen on the eastern side of the Gulf of Alaska

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(divergence) at a coast or in midocean. In the following discussion it will be convenient to use the term 'Sverdrup unit' to indicate a flow of one million cubic metres per second.

According to the map on this page Ekman transport removes water from the equatorial currents and the northern gyre and transports it into the central gyre. Some 45 streamlines enter the gyre at its perimeter (from the coasts, between islands and across 10° and 50°N). What happens to this massive flow? Most of it—about 40 Sverdrup units—evaporates into the cool, dry air flowing out of the atmospheric high. But Ekman transport more than makes up for this loss; the excess 'piles up' in the Subtropical Convergence and sinks to depths of 100 to 200 metres. From there, much of this water spreads radially outward but some of it is mixed downward, warming the underlying water. Over long periods of time, a 'lens' of lower density water about one kilometre thick has accumulated in the centre of the gyre. The low density layer is only one quarter to one-tenth as thick at the perimeters of the gyre, and cold dense, deep water is found much closer to the surface there.

Density gradients due to convergence and divergence of the Ekman transport cause horizontal pressure gradients which generate the geostrophic flow shown on the map on page 59. Such gradients are largest in the upper 100 to 200 metres and diminish to negligible values at 1 to 2km depth, due to compensating displacements of denser, deep water.

The effectiveness of coriolis force in limiting the flow of water out of the thick, warm water lens at the convergence can be understood by comparing currents and horizontal pressure gradients in the central gyre with those at the Equator, where coriolis force vanishes. At the Equator a pressure gradient only one per cent as strong as that across the Kuroshio produces comparable current velocities. Why? Because flow at the Equator is not geostrophic and is therefore free to speed up until friction and inertia forces are large enough to balance the pressure gradient. At higher latitudes coriolis force allows much larger horizontal pressure gradients to build up before the flow reaches speeds where friction and inertia forces become important limiting factor.

The potential energy stored in the mid-latitude gyre is many hundreds of times greater than the kinetic energy of its currents, and represents an accumulation of energy five to ten times larger than the energy added by winds in a year. It is not surprising, then, that the ocean's density structure is remarkably constant, and that currents such as the Kuroshio hardly respond to changes in the local winds. Currents near the Equator, on the other hand, represent much smaller accumulations of energy and respond much more readily to changes in the wind.

AFTER DECADES of effort by Japanese oceanographers, supplemented by studies made during international expeditions and by individuals from many countries, it is now possible to piece together a reasonably satisfactory description of the Kuroshio proper. Water enters the Kuroshio over a broad front 1000km in width (13°N to about 23°N at longitude 125°E) then accelerates and narrows. Some water leaves the right hand side of the Kuroshio as soon as it begins to turn towards the east, but narrow, intense flow persists for 1500 to 2000km after the current leaves Japan's east coast, after which there is a marked drop in velocity. This region of narrow intense flow east of Japan is called the Kuroshio extension, and it differs from the Kuroshio in that there is no land boundary on the left hand side to generate a frictional boundary layer.

Comparison of velocity profiles (plots of velocity across the surface current) of the Kuroshio and the Kuroshio extension shows that, although both have essentially identical velocity profiles on their right hand sides, the velocity gradient on the left hand side of the

Kuroshio is at least six times greater (a change of 2m/s in 8km) than that in the Kuroshio extension (2m/s in 50km). Other things being equal, this would result in six times greater frictional stress on the left side of the Kuroshio. Such velocity profiles support the theoretical view that the Kuroshio and Kuroshio extension are the major nongeostrophic portions of the flow in the central and northern gyres, where important adjustments in the distribution of energy take place.

In the Kuroshio energy is dissipated through friction (on a small scale, since the frictional boundary layer is only about ten kilometres wide). On average, the dissipation rate must be in balance with the mean rate at which wind adds energy to the central gyre.

However, friction not only dissipates energy, it also generates counterclockwise angular momentum at a rate which more than compensates for the decrease in the Earth's (counterclockwise) angular momentum as the current flows north. To balance this excess, clockwise angular momentum is generated on the right hand side of the current, where the velocity decreases towards the right in what is sometimes termed an inertial boundary layer. As H. Stommel pointed out in 1948, this balance of angular momentum can only be attained on the western boundary, which accounts for the westward intensification in the current systems of the world oceans.

In the Kuroshio extension the flow adjusts to conditions in the ocean's interior, where large velocity gradients, and the angular momentum associated with such gradients, cannot persist. Friction is no longer concentrated at the boundary, nor are inertial forces restricted to the right hand side of the stream. Instead, large eddies and meanders dissipate kinetic energy throughout the path of the flow, and redistribute angular momentum at the same time. The transport decreases downstream as the flow fans out and becomes the broad, slow West Wind Drift between 155° and 160°E.

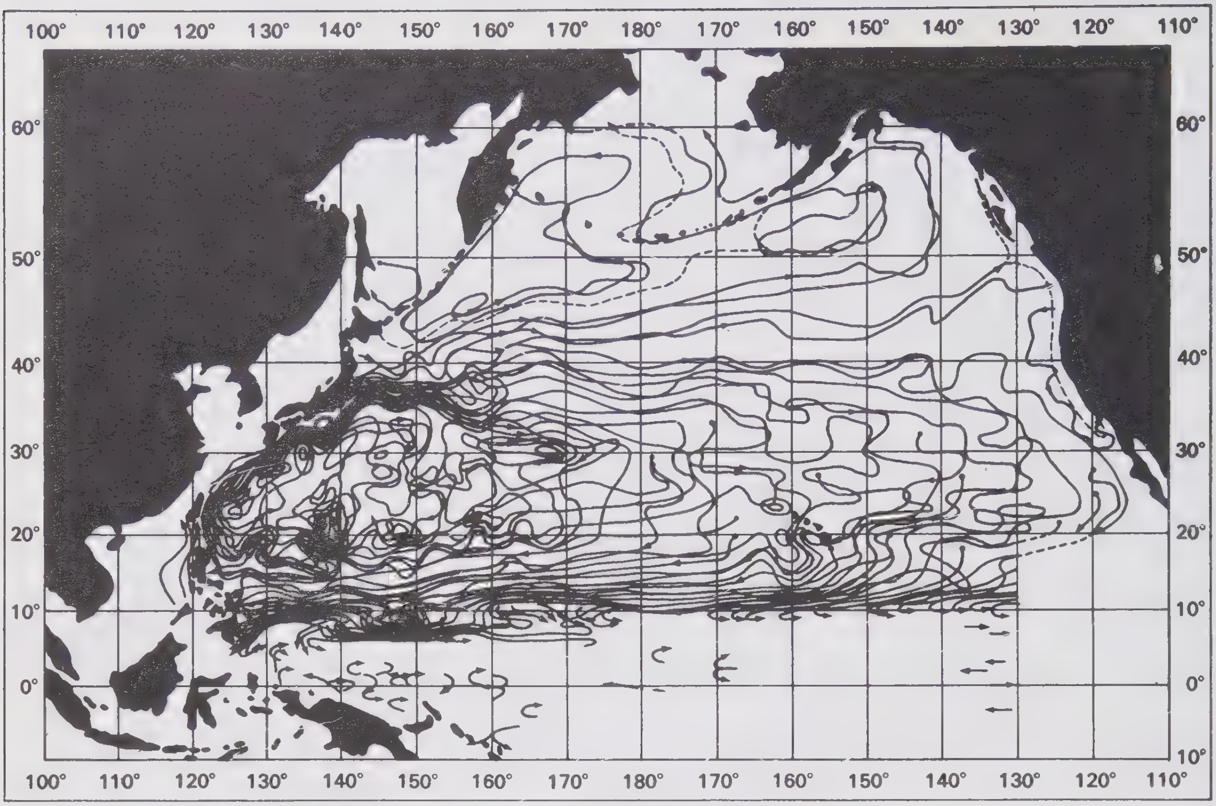
Fifty Sverdrup units of flow approach the east coast of Mindanao in the Philippines and half of this volume turns north into the Kuroshio. Most of this flow consists of warm (20°-28°C) water in the upper 200 metres; there is a layer with relatively high salinity (near 35 parts per thousand) between 100 and 200 metres with slightly more dilute water (34.5 parts per thousand) above that.

The depth of the high velocity flow increases from 200 to 400 metres, and the velocity goes up from a few tens of centimetres per second to one metre per second as the current narrows east of Taiwan. From Taiwan to Japan some dilute water from the Asian shelf, on the left of the current, is entrained by the flow, which speeds up even more, to velocities of 1.5 to 3m/s. Transport just off Japan's south coast amounts to 35 Sverdrup units, but there may be significant flow below 1000 metres since the current extends to considerable depths at that point, and so the total transport may be as high as 45 to 50 Sverdrup units.

Just as the current reaches Japan's southeast tip, it flows over the shallow Izu-Bonin Ridge which extends due south from Honshu, Japan's main island. The Kuroshio undergoes complex and little understood fluctuations near this ridge.

Once past the Izu-Bonin Ridge, the Kuroshio may turn north along Japan's east coast for a short distance, or it may continue to flow almost due east. In either case, it joins the Oyashio current, which flows southward from the Kamchatka Peninsula. Together these two currents leave the coast and form the Kuroshio extension. Transports here amount to about 45 Sverdrup units (up to 60 on occasion) though only 25 to 35 Sverdrup units are within the high

MACKEREL FISHING FLEET from Choshi heading for the rich fishing grounds of the Kuroshio extension. Some boats spend 80 per cent of their time scouting for fish, but improved knowledge of the current could reduce this time, and so increase their catch



TOTAL TRANSPORT by geostrophic currents in the north Pacific. Transport in the upper 1000 metres is shown in colour (each line represents 5 Sverdrup units), and in the upper 100 metres in black (each line represents 1 Sverdrup unit). The map shows the intense narrow flow at the western boundary, the change to broad slow moving flow downstream, near longitude 160°E, and the even broader slower moving water transport which occurs toward the south

velocity core of the Kuroshio extension, where speeds of two metres per second or more are often observed.

By the time the current has reached 160°E, towards the end of the Kuroshio extension, it consists of a mosaic of water types: warm saline water from the original source off the Philippines, coastal and shelf water of lower salinity, and cold dilute water from the Oyashio, with summer temperatures of 3° to 10°C, and salinities sometimes as low as 33.8 parts per thousand.

Some mixing occurs in the core of the Kuroshio extension, but on the whole there are two distinct types of water in the current: warm saline water on the right, and cold dilute water on the left. The convoluted front separating these two types of water is often very sharp and active, with strong velocity gradients and shape contrasts in the properties of the water on the two sides. Rich fishing grounds are located on both sides of the frontal zone in the Kuroshio extension, so this complex feature of the western north Pacific is of particular interest to Japan's fishing fleet. A pioneer in fisheries oceanography, Professor Michitaka Uda, has studied such fronts and the fisheries associated with them since 1930. He and his colleagues in Japan's unique system of fisheries universities have contributed much to our knowledge of the sea as an environment. They have taken particular interest in variability in the occurrence of various kinds of fish, and changes in the environment which cause much of this variability.

The path of the Kuroshio as shown in the map on page 55 is very nearly its average position, but the current can undergo marked and fairly rapid changes in speed and in the location of its axis. Apart from changes due to tides, short term changes due to major shifts in the axis of the Kuroshio can occur as it flows past southern Japan. Meanders develop in the current which occasionally bring high velocity flow unusually close to the coastline, and part of the Kuroshio's flow may be diverted into nearby bays, where it can flush out much of the coastal water within a matter of days. These sudden and as yet unpredictable events cause widespread damage to boats and fishing gear anchored in the normally quiet waters, as offshore currents move inshore at speeds of 1-2 m/s, or more.

Meanders in the Kuroshio south of Japan have been studied intensively. The axis of the current may shift onshore or offshore 100km or more in a matter of weeks. For example, in 1959 the Kuroshio off Japan's south coast (at 133°E) began to move offshore in March or April, shifting from its initial position 20km offshore to a distance of 140km in about one month. This meander also drifted rather slowly downstream, reaching the central portion of the south coast (136°E) by the end of May and the eastern portion (139°E) by early August, at which time the Kuroshio's axis was back within 25 Km of the coast farther upstream (133°E), where the disturbance was first observed. Such meanders may appear and disappear within a few months, but they may also remain more or less stationary for more than a decade. When the meander develops, cold water is brought up toward the surface between the Kuroshio and the coast and temperatures drop to as much as 10°C below normal. This change has profound effects on coastal and offshore fisheries, since the area involved is fairly large—about the size of the Bay of Biscay. Familiar species of fish move away and are replaced by others, and so fishermen must either move to new grounds or market what they can catch on the old grounds.

The only nontidal changes in the Kuroshio which appear to be at all regular are annual changes in velocity and transport, which are easily obscured by the irregular variations discussed above. Japanese scientists generally agree that the speed is greatest from May until August, with a second maximum in January and February. But an analysis by Y. V. Pavlova has shown that the annual cycle is rather more complex, at least for geostrophic currents. Speed and transport not only vary with season, they vary in different ways from place to place along the Kuroshio. Off the southern tip of Japan, for example, maximum transport within the Kuroshio occurs in September and again in March or April, while maximum velocities are observed in July and January. Just east of Japan, according to Pavlova, maxima in transport occur during June and December, with velocity maxima in August and February.

WHAT NOW REMAINS to be learned about currents such as the Kuroshio? Perhaps most valuable would be information on fine structure and on fluctuations over periods of a month or less. To determine how fluctuations propagate from place to place, measurements must be made simultaneously at several points along the current, and at least a few direct measurements must be made of the currents at all depths. Many developments in ocean current theory await the results of such observations, which will also be needed for forecasts of conditions in and near the Kuroshio to serve the needs of fishermen and meteorologists. But the effort required, for a complete survey of the Kuroshio, in terms of ships, time and operating costs, is staggering and detailed rapid surveys of the Kuroshio must wait until more efficient tools, such as instrumented buoys, become commonly available.

Once routine monitoring of the marine environment becomes commonplace, we can expect marked improvements in long range weather forecasts and in catch rates of commercial fisheries, which will rapidly repay the original investment of effort and funds. Even rather minor improvements in weather forecasts can bring significant savings to farmers, public utilities, cargo ships, airlines and others who use forecasts in scheduling operations or planning routes.

Farmers in northern Japan may have good or poor harvests depending on the extent to which the Kuroshio flows north along Japan's east coast, before joining the cold Oyashio water, since water temperatures offshore strongly influence cloud cover and rainfall. Similarly, cold air from Siberia flows out over the Pacific in winter, to encounter warm water carried north by the Kuroshio; these temperature contrasts trigger formation of numerous cyclonic lows in the atmosphere over the Kuroshio. The lows carry stormy weather east to northeast across the northern Pacific Ocean towards the coasts of Alaska, Canada and the United States.

Improved knowledge of the ocean as an environment can help fishermen locate and catch protein to feed an increasingly hungry world. Fishermen could make direct use of forecasts of the Kuroshio's flow, because the entire current system is a series of fishing grounds which move about with changes in the flow. Various species of tuna, sardine and anchovy, mackerel, squid and many other commercially important species are each found in specific zones in and near the Kuroshio. For example, fronts where coastal and offshore waters meet are often good fishing grounds. Species such as sardines are caught on the coastal side of these fronts, while mackerel and tuna occur in abundance in the warmer offshore waters. Changes in the marine environment appear to influence both the timing and the paths of fish migrations.

For more than 50 years, Kitahara, Uda and their fellow fisheries oceanographers in Japan have studied the response of fish to their environment. They have set up an extensive network for collecting and reporting temperatures at the sea surface and at various depths, movements of schools of fish near various fishing grounds, catch rates, and ocean current information for making fishing condition forecasts.

Six regional fisheries research laboratories and 38 prefectual fisheries experiment stations are responsible for collecting, analysing and distributing information on individual fisheries, such as the salmon, sardine or albacore. Ships at sea send information on their catches and the environment to the appropriate laboratory by radio. There these reports are compiled and analysed to produce charts of fishing conditions, conditions in the ocean, and forecasts of various kinds, which are sent to the fishing fleet by mail, radio and facsimile. Some charts and forecasts are prepared at 10 day intervals, and others are sent out once a month. Research and cargo ships also provide information on temperature, salinity, currents and other factors in the environment for use in the fishing condition broadcasts.

Forecasts are based on long term trends, the time when fishing begins or ends on various grounds, data on age and size composition of the catch, and on experience with changes in the ocean in various fishing areas and the consequences of such changes in the past. It is still too early to evaluate the system's effectiveness, except to note that the information provided to the fishermen is very much in demand.

The potential value of fishery forecasting systems can be judged from the fact that boats in some fisheries must spend 80 per cent or more of their time scouting for fish. If this time could be reduced by half, each ship in such a fishery could increase its catch as much as threefold.

We have seen that there are many reasons for undertakings such as the Co-operative Study of the Kuroshio. They range from the most abstract, through the coldly practical to the mundane—improvements in ocean current theory, better weather predictions, more efficient ways to catch fish, and improved charts of the oceans. All these and more will result from studies of the Kuroshio and other parts of the world ocean. But regardless of motive, form or content, the goal of these studies can be summarized in much simpler terms: the search for man's ultimate tool, knowledge.

FURTHER READING

WATER CHARACTERISTICS OF THE KUROSHIO by J. Masuzawa (in *The Oceanographical Magazine, 17, 37, 1965*)

THE SEASONAL VARIATION OF THE KUROSHIO CURRENT (In Russian) by Y. V. Pavlova (in *Okeanologia, 4, 625, 1964)*

DESCRIPTION OF THE KUROSHIO (PHYSICAL ASPECT) by D. Shoji (in *Proceedings of Symposium on the Kuroshio, Oceanographical Society of Japan and UNESCO, Tokyo, 1965*)

ON THE VARIABILITY OF THE VELOCITY OF THE KUROSHIO VOL 1 by D. Shoji and H. Nitani (in *The Journal of the Oceanographical Society of Japan, 22, 192 1966*)

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ON THE NATURE OF THE KUROSHIO, ITS ORIGIN AND MEANDERS by M. Uda (in *Studies on Oceanography Hidaka Jubilee Committee, Tokyo, 1964*)

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7303

RESPIRATORY RESPONSE OF JUVENILE CHINOOK SALMON AND STRIPED BASS EXPOSED TO BENZENE, A WATER-SOLUBLE COMPONENT OF CRUDE OIL

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ABSTRACT

Interest surrounding the potential effects of crude oil on aquatic organisms has increased in recent years due to the incidence of accidental oil spills. There are few experimental results reported, however, dealing with the effect on aquatic species of water-soluble aromatic hydrocarbons contained in crude oil. Such compounds are highly toxic to mammals.

Experiments were conducted using juvenile chinook salmon, Oncorhynchus tshawytscha, *and striped bass,* Morone saxatilis. *The fish were exposed to sub-lethal concentrations of the aromatic hydrocarbon benzene, for periods ranging from 1-96 hours. Prior to exposure, and after exposure to the benzene, respiration rates of individual fish were measured. Results show increases in respiratory rate up to 115 percent above that of control fish after exposure periods of 24 hours for striped bass and 48 hours for chinook salmon. Fish exposed to benzene concentrations of 10 ppm for periods longer than those listed exhibited a narcosis that caused a decrease in respiratory rate. The narcotic state induced by exposure to benzene was shown to be reversible when the fish were placed in fresh water and kept for periods longer than 6 days. Possible biochemical mechanisms leading to this response are hypothesized.*

INTRODUCTION

Interest surrounding the potential effects of crude oil on aquatic organisms has increased in recent years due to the incidence of accidental oil spills from vessels, oil terminals, and offshore drilling operations. There is extensive documentation in the literature of the effects of tar components on aquatic organisms[1,2] and researchers are beginning to investigate the accumulation and translocation through aquatic systems of hydrocarbons associated with crude oil. There are few experimental results reported however, dealing with the effects on aquatic species of water-soluble aromatic hydrocarbons contained in crude oil.

While the holistic approach to subjecting organisms to crude oil in total is desirable, the results are difficult to analyze for cause and effect relationships and it is impossible to examine for differential toxicity of the various components. Our laboratory has therefore, begun a systematic examination of those compounds thought to be most toxic to fish: the low-boiling point aromatic compounds.

Among the aromatic compounds, benzene is high in relative abundance, constituting 20 percent or more of the total aromatics in crude oil. A second reason for choosing benzene for investigation is its high degree of water-solubility (in excess of 200 ppm).

Manifestation of the effects of environmental factors are expressed in the physiological state of the organism and in the production of the population. Respiratory metabolism as a measure of the physiological state of fish has been proved to be a sensitive parameter in evaluating stress caused by a variety of environmental variables[3,4,5,6,7]. The relationship of standard metabolism to energy utilization in fish is well represented in the balanced equation presented by Warren and Davis[8]. The cost in energy of standard metabolism is considered to be the minimal level of physiological and mechanical work necessary to maintain an organism. Any increase in this cost will reduce the amount of energy available for other fates such as growth and there will occur a resultant decrease in production over time in the absence of other compensatory mechanisms.

I have therefore chosen respiratory rate as an appropriate and sensitive parameter to evaluate potential stress caused by sub-lethal concentrations of benzene. These experiments were conducted using juvenile chinook salmon, *Oncorhynchus tshawytscha*, and juvenile striped bass, *Morone saxatilis*. The fish were exposed to sub-lethal concentrations of benzene for varying periods of time. After exposure to the benzene, standard metabolism was measured using tunnel-type continuous flow respirometers. This research was conducted in association with the Department of Animal Physiology, University of California at Davis, from April through September 1972.

Methods and Materials

Juvenile chinook salmon used in this study were obtained from the Bureau of Sport Fisheries and Wildlife's Coleman Hatchery, located near Red Bluff, California. All salmon used in this study were under-yearlings ranging in weight from 2.10 to 5.90 grams (Table 1). The fish were selectively sorted for uniform size and held in well-aerated 200-gallon tanks at 16± 1°C. During the period of acclimation (two weeks) and also during the periods of exposure to benzene, the fish were fed commercially obtained tubificid worms of the genus *Tubifex spp.*

Striped bass used in this study were obtained from the water diversion facilities of the Bureau of Reclamation, located near Tracy, California. The striped bass were not as uniform in size as the salmon, ranging in weight from 33.13-67.62 grams (Table 1). The striped bass were held under the same laboratory conditions and fed the same food type as the salmon.

Water used in the experiments and for holding fish was supplied by a well, the quality of which is reported by Kruger[9]. Water was continuously exchanged in the holding tanks at the rate of 2 liters per minute and filtered through glass wool and activated charcoal filters. Banks of daylight fluorescent lights operated through time switches provided controlled illumination and day length was adjusted weekly to correspond to the natural photoperiod.

Exposure to Benzene

All exposure experiments were conducted in 15-gallon glass aquaria under static water conditions. Each aquarium was divided into three chambers measuring approximately one cubic foot. Each chamber was aerated and used to hold

Table 1: Summary of Experimental Conditions and Experimental Animals Used in These Studies.

Benzene concentration (ppm)	Water velocity (cm/sec)	Length of exposure (hours)	Number of fish	weight of fish (grams wet)	
				Range	Mean
Chinook Salmon					
5	7	1	5	4.32- 5.91	4.87
5	7	24	5	5.16- 5.70	5.54
5	7	48	5	3.63- 4.79	4.08
5	7	72	5	4.36- 5.24	5.02
5	7	96	5	3.30- 4.07	3.94
5	14	1	5	4.32- 5.91	4.87
5	14	24	5	5.16- 5.70	5.54
5	14	48	5	3.63- 4.79	4.08
5	14	72	5	4.36- 5.24	5.02
5	14	96	5	3.30- 4.07	3.94
10	7	1	5	4.80- 5.02	4.94
10	7	24	5	3.33- 5.10	4.51
10	7	48	5	2.15- 3.20	3.04
10	7	72	5	4.17- 4.89	4.46
10	7	96	5	2.55- 3.08	2.97
10	14	1	5	4.80- 5.02	4.94
10	14	24	5	3.33- 5.10	4.51
10	14	48	5	2.15- 3.20	3.04
10	14	72	5	4.17- 4.89	4.46
10	14	96	5	2.55- 3.08	2.97
control	7	1-96	16	4.00- 5.58	4.32
control	14	1-96	16	4.00- 5.58	4.75
Striped bass					
5	7	24	5	36.78-47.88	45.33
5	7	48	5	43.08-67.62	51.90
5	7	72	5	38.68-46.23	43.43
5	7	96	5	36.70-49.40	40.98
5	14	24	5	36.78-47.88	45.33
5	14	48	5	43.08-67.62	51.90
5	14	72	5	38.68-46.23	43.43
5	14	96	5	36.70-49.40	40.98
10	7	24	5	41.64-65.66	49.78
10	7	48	5	31.67-43.74	38.03
10	7	72	5	39.14-51.62	45.33
10	7	96	5	33.61-45.16	39.13
10	14	24	5	41.64-65.66	49.78
10	14	48	5	31.67-43.74	38.03
10	14	72	5	39.14-51.62	45.33
10	14	96	5	33.61-45.16	39.13
control	7	24-96	20	33.13-56.63	44.60
control	14	24-96	20	33.13-56.63	44.60

a single fish. Dissolved oxygen and temperatures were monitored on an hourly basis averaging 9.2 mg/l and 16± 1°C respectively. Dissolved oxygen levels never dropped below 7.8 mg/l.

Benzene concentrations used were 0, 5, and 10 ppm. Preliminary acute toxicity bioassays produced mortality at 15 ppm benzene (by volume). It is probable that concentrations in the range of 0-15 ppm would exist in the vicinity of an oil spill in fresh or salt water considering the relative abundance of benzene in most crude oils (20 percent or more of total aromatics) and its high solubility in water (in excess of 200 ppm).

Benzene concentrations were derived on a volume basis by the following procedure: Reagent benzene was introduced by syringe into a 200 ml water sample held in a glass-stoppered reagent bottle. The sample was then stoppered and shaken for 15 seconds to emulsify the benzene in the sample. The emulsified sample was then poured into the test aquaria so as to equally distribute the benzene amongst the chambers. Each chamber was stirred with a glass rod for 10 seconds to distribute the benzene in the water column. During each exposure experiment, the above procedure was repeated every 48 hours, with the exception that one-half the water volume in each aquarium was removed and replenished. Analyses for benzene concentration were performed using gas liquid chromatography.

The test fish were placed in the aquaria prior to introduction of the benzene and allowed an acclimation period of 48 hours. After exposure to benzene, which ranged in time from 1-96 hours (Table 1), the fish were removed and placed in the respirometers for measurement of respiratory metabolism.

Respirometry

Six recirculating tunnel respirometers were used in this study and were modified from similar apparatus used by Brett[10] and Averett[6]. A detailed explanation of the operating mechanisms can be found in Kruger[9]. Briefly, the respirometers consisted of a plexiglass tube, 6.3 cm long (Fig. 1). Two plexiglass baffles were situated 4 cm apart at the front end of the tube. Turbulent water entering the tube was channeled into an essentially rectilinear flow by these baffles. At the rear of the tube, a 0.6 cm mesh stainless steel screen formed a barrier to prevent fish from being sucked into the pumps. Water entered and left the respirometers through 2.5 cm openings in the expansion and reduction cones which were bolted over the ends of the respiration tube.

Oxygen consumption of the experimental fish was taken to be the difference between the dissolved oxygen content of the water in the respirometer from one point in time to another (usually 15 minutes), during which time the respirometer was sealed from any exogenous source of gas or liquid exchange. At the beginning of each test, a water sample was taken from the flushing-sampling outlets, then both the inlets and outlets were sealed. After the 15 minute time interval, a terminal water sample was taken in a 125 ml glass stoppered bottle. Analyses for dissolved oxygen was made using the Azide modification of the Winkler method[11].

After each fish was exposed for the appropriate period of time to benzene, it was removed from the aquarium, placed in the respirometer and allowed to acclimate for at least 12 hours prior to the first oxygen consumption measurement. This procedure was followed to allow excitement in the fish due to handling to subside. All fish were weighed prior to and immediately after each experiment and all weights reported are initial wet weights unless otherwise stated. Experiments were conducted at two water velocities; 7 and 14 cm/second to test the ability of the fish to increase their activity level after exposure to benzene.

The striped bass used in this study were not as uniform in size as were the salmon. This was because the salmon were supplied from a hatchery but it was necessary to collect the striped bass from the field and only a wide range in sizes was available (Table 1). Because of this range in sizes, it was necessary to determine the relationship between respiration rate and body weight of striped bass. This was done in order to derive values of standard metabolic rate for striped bass exposed to benzene. The difference between the metabolic rate exhibited by a fish after exposure to benzene and the standard metabolic rate derived from the relationship shown in Fig. 2 was taken to be the response caused by the benzene. It was then possible to calculate the percent increase in respiration by dividing the difference by the value for standard metabolic rate derived from Fig. 2.

Results and Interpretation

Exposure to 5 ppm benzene caused an increase in the respiration rates of juvenile chinook salmon irrespective of the length of time of the exposure (Fig. 3). However, the magnitude of the increase did appear to be related to the length of the exposure time. The greatest percent increase (86 percent) occurred after an exposure time of 48 hours, becoming less accentuated at exposure periods of 72 and 96 hours (Fig. 3). The same general relationship between percent difference in respiration rate of control fish and fish exposed to 5 ppm benzene was exhibited when salmon were exposed to 10 ppm benzene (Fig. 4). The increase in respiration rates was greater at every exposure period except 96 hours. The mean increase in respiration rate of salmon exposed to 10 ppm benzene for 48 hours was 115 percent. The oxygen consumption rates of all fish expressed as mg O_2/kg/hr are given in Table 2. There did not appear to be a significant difference between the response of fish held at the two different water velocities. The 14 cm/sec water velocity was near the flow capacity of the respirometers used, but well below the swimming abilities of the juvenile salmon. Dahlberg, et. al.[12] found juvenile coho salmon ranging in size from 4.3 to 6.6 grams to be able to swim at speeds greater than 66 cm/sec. I believe, therefore, that the difference between 7 and 14 cm/sec was insufficient to cause a significant increase in the activity of the salmon.

When the difference in respiration rate of striped bass exposed to 5 ppm benzene is plotted against the length of exposure (Fig. 5) the resultant relationship is different than that of the salmon (Fig. 3). The largest increase was exhibited at 24 hours by the bass where it was elicited at 48 hours in the salmon. The magnitude of the increase was not as great in the bass as it was in the salmon; the greatest increase being 45 percent. As can be seen in Figure 5, the difference in respiration rate was least at the 48 hour exposure period at a water velocity of 7 cm/sec. Contrary to the response of the salmon to the two current velocities, the striped bass appeared to have a distinct response to benzene at water velocities of 7 and 14 cm/sec (Fig. 5). The mean values have been plotted showing 2 standard errors. This separation at the two water velocities may be due to the relative poor swimming ability of the striped bass in comparison to the salmon. Painter and Wixom[13] have shown striped bass to be poor swimmers and found fish of 41 to 70 cm in length to be able to swim at velocities of 60 cm/sec for only a few minutes. Therefore, a difference in 7 cm/sec water velocity could be sufficient to cause an increased stress on the fish after exposure to benzene.

The response of striped bass exposed to 10 ppm benzene (Fig. 6) is much different than any of those previously discussed. The respiration rate of the striped bass decreased at both 7 and 14 cm/sec when exposed for 24 hours. At 7 cm/sec and an exposure time of 48 hours, respiration rate was depressed even more but the depression was not as great with exposure times of 72 and 96 hours. At a water velocity of 14 cm/sec., the depression in respiration rate occurred only with the 24 hour exposure period, the rate being increased at the other exposure periods (Fig. 6). I believe this difference in response is due to the gill flushing rate and metabolism of the benzene within the fish and this will be treated in detail in the Discussion section.

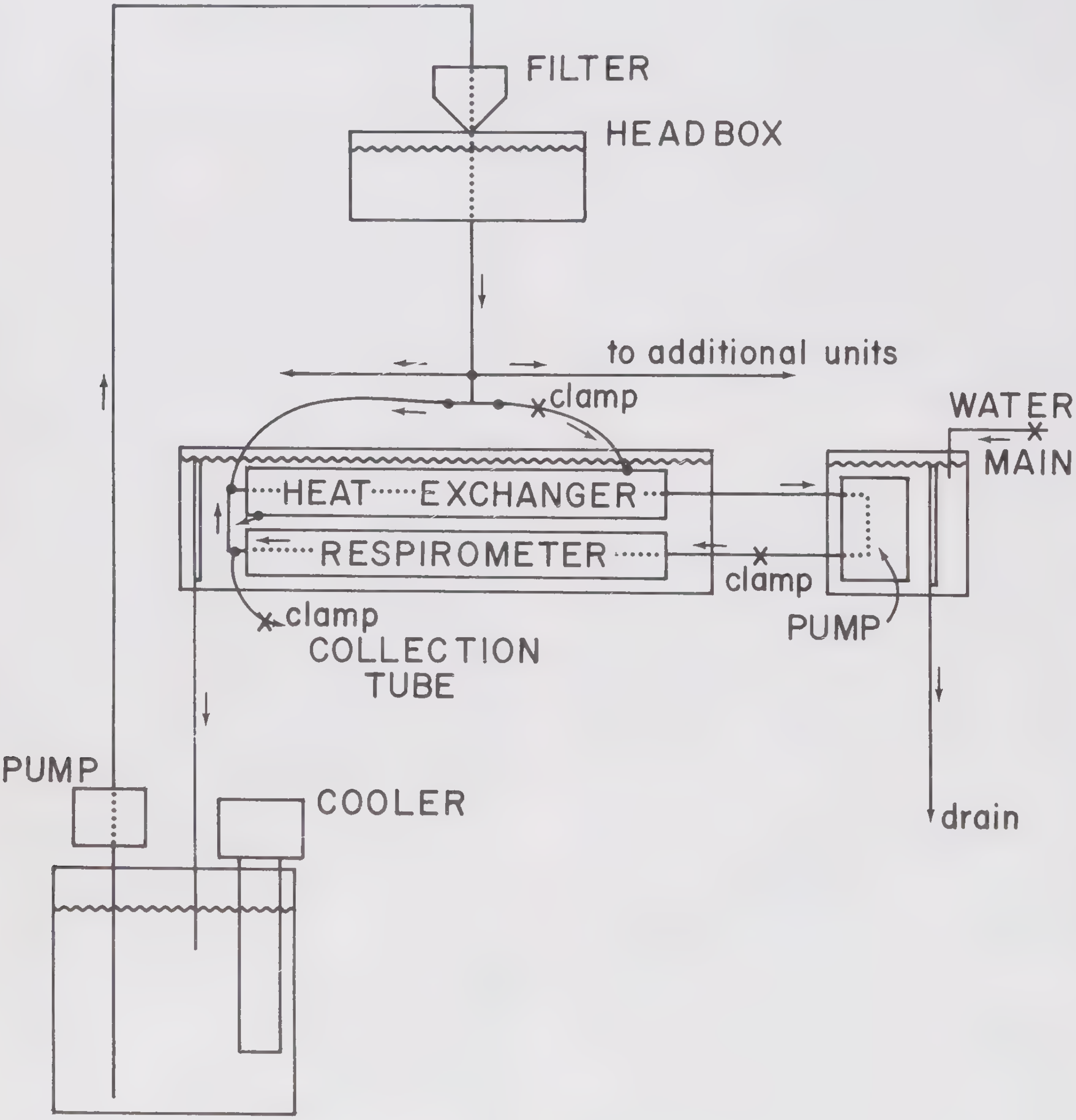
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Figure 1: Diagram of One of the Respirometers Used in This Study.

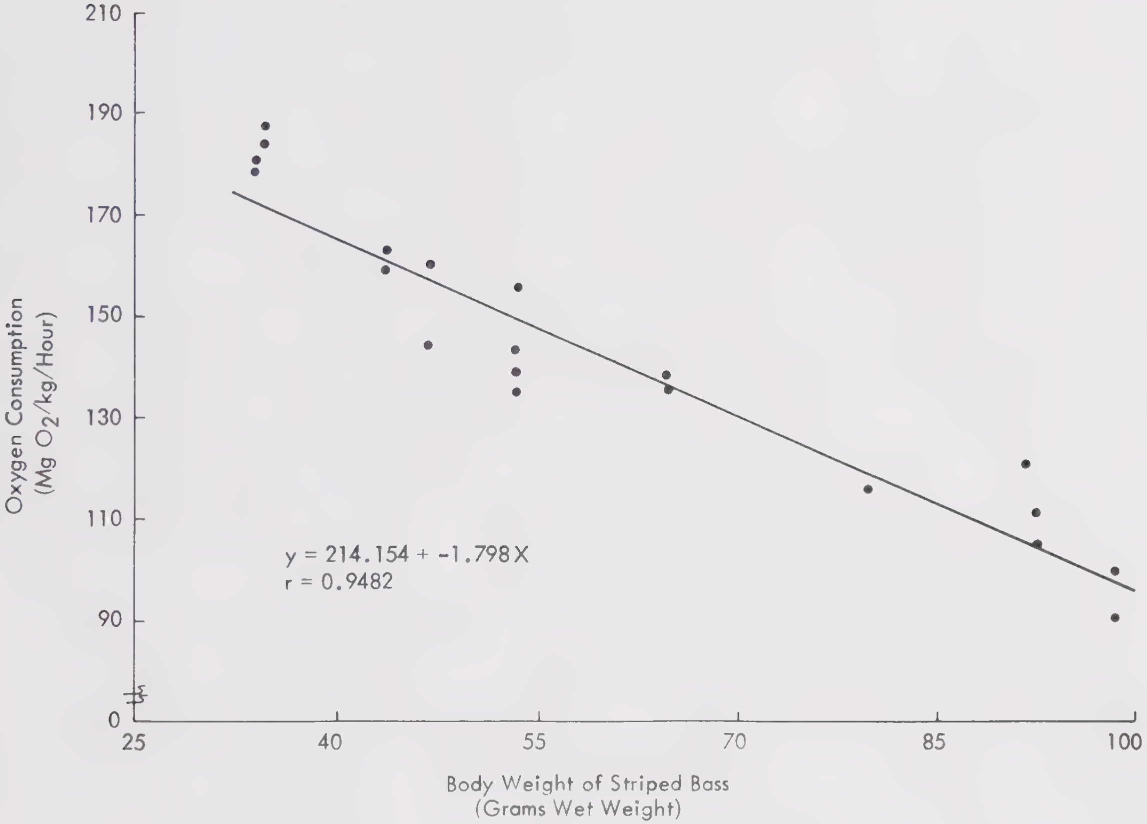

Figure 2: Relationship Between Rate of Oxygen Consumption and Body Weight of Striped Bass.

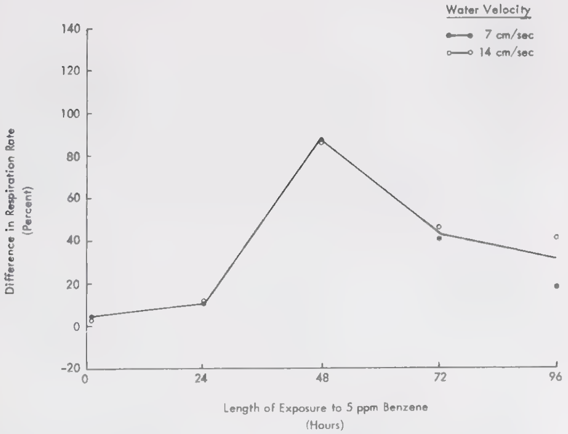

Figure 3: Relationship Between Percent Difference from Control Fish in Respiration of Juvenile Chinook Salmon Exposed to 5 ppm Benzene and Length of Exposure. Each Point Represents the Mean Value for 5 Fish.

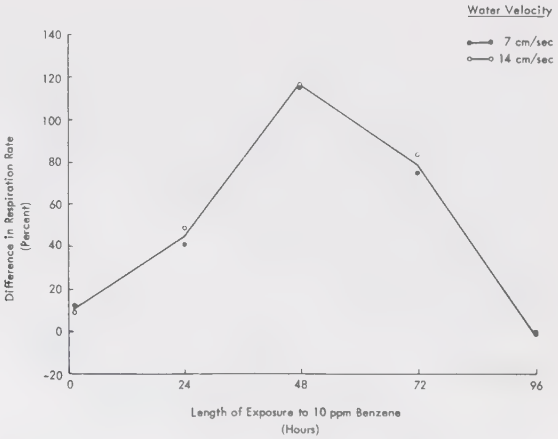

Figure 4: Relationship Between Percent Difference from Control Fish in Respiration of Juvenile Chinook Salmon Exposed to 10 ppm Benzene and Length of Exposure. Each Point Represents the Mean Value for 5 Fish.

Table 2: Summary of Respiration Rates Derived for Experimental Fish.[1]

Benzene concentration (ppm)	Water velocity (cm/sec)	Length of exposure (hours)	Respiration Rate (mgO_2/kg/hr) $\bar{x}$ standard	$\bar{x}$ after exposure
Chinook Salmon				
5	7	1	231.00	241.20
5	7	24	231.00	254.40
5	7	48	231.00	431.40
5	7	72	231.00	323.70
5	7	96	231.00	272.40
5	14	1	240.00	246.00
5	14	24	240.00	268.20
5	14	48	240.00	445.20
5	14	72	240.00	349.30
5	14	96	240.00	336.60
10	7	1	231.00	259.2
10	7	24	231.00	325.2
10	7	48	231.00	495.0
10	7	72	231.00	401.3
10	7	96	231.00	229.80
10	14	1	240.00	261.60
10	14	24	240.00	356.40
10	14	48	240.00	517.80
10	14	72	240.00	438.10
10	14	96	240.00	237.60
Striped bass				
5	7	24	158.67	205.50
5	7	48	150.20	140.60
5	7	72	161.20	138.94
5	7	96	164.60	169.18
5	14	24	156.80	227.13
5	14	48	151.17	150.36
5	14	72	158.80	162.12
5	14	96	164.60	181.12
10	7	24	154.00	132.40
10	7	48	167.20	137.14
10	7	72	158.20	145.14
10	7	96	166.60	164.34
10	14	24	154.00	148.86
10	14	48	167.20	179.46
10	14	72	158.20	173.96
10	14	96	166.60	190.32

[1] Each value is a mean of 5 fish. Values for individual fish based upon 8 determinations.

Gill tissue of some of the experimental fish exposed to the benzene was examined for histological damage and none was found. To examine the question of the duration of the response elicited by a single exposure to a concentration of benzene, both salmon and striped bass were exposed to a concentration of 10 ppm benzene for a period of 24 hours. The fish were then placed in clean water and held for a period of ten days, during which their respiration rates were measured every two days at a current velocity of 14 cm/sec.

The results of these tests are shown in Fig. 7. Although the initial respiratory response was different between the salmon and the striped bass, the respiration rate returned to normal in both species at the end of the ten day period following exposure.

DISCUSSION

Benzene is absorbed across the gill surface of fish directly into the blood. Being lipid-soluble, the benzene attaches to erythrocytes and, to a lesser degree, the lipoproteins in the blood[14]. It is then transmitted via the blood for deposit in the tissues or undergoes bio-oxidation to phenol in the liver and other tissues. Some benzene is excreted across the gills in unchanged form. Some hydroxylation of benzene to phenol occurs in the kidney and muscle tissue[15,16]. Common to all of these pathways is the fact that the reaction is enzymatic and requires $NADPH_2$ and O_2. This is the same biological pathway followed in the hydroxylation of steroids and pre-oxidation of lipids. Since this is the case, the amount of foreign chemical that can be oxidized is proportional to the amount of $NADPH_2$ and O_2 available. If lipid oxidation and the hydroxylation of benzene were occurring at the same time, there could exist a competitive inhibition, and neither compound would be likely to be fully metabolized, thus allowing for a build-up of benzene in lipid-rich nervous tissue. If we examine the respiratory responses of the experimental fish shown in Figures 3-7, I believe we can see evidence of the above phenomenon.

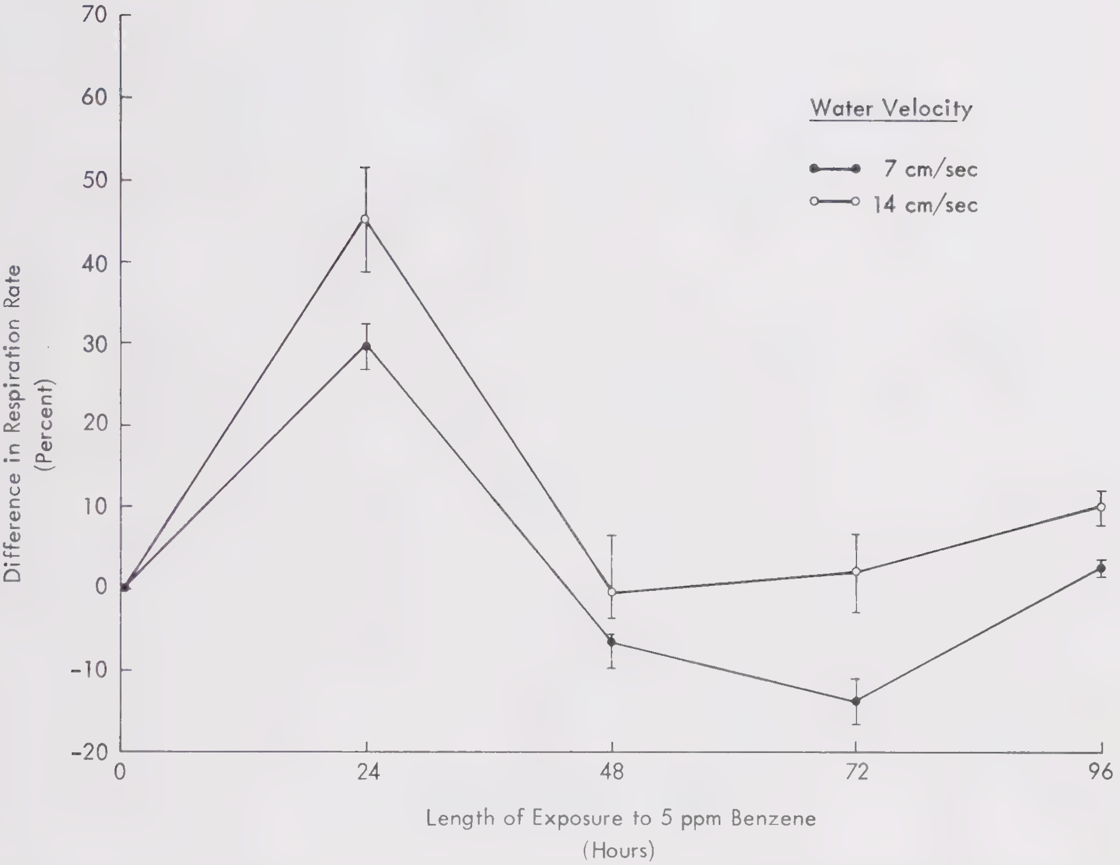

Figure 5: Relationships Between Percent Difference from Control Fish in Respiration of Juvenile Striped Bass Exposed to 5 ppm Benzene and Length of Exposure. Each Point Represents the Mean Value for 5 Fish with 2 Standard Errors Shown.

The juvenile chinook salmon exhibited an increase in respiratory rate at both the 5 and 10 ppm concentrations of benzene (Figures 3 and 4). I believe this increase in respiration to be due to the increased need for oxygen to metabolize the benzene via the pathway previously discussed. The difference in the magnitude of the increase between the two concentrations is probably proportional to the oxygen demand for metabolism. The decreased level of respiration at exposure periods of 72 and 96 hours, even though greater than control values, could be due to an inability of the fish to retrieve sufficient oxygen to fully metabolize the benzene, thus causing an accumulation of benzene in the nervous tissue and resultant narcosis. Such a narcotic effect is well-documented for benzene in mammals[14], and could act in a similar manner in fish due to the particular metabolic pathway under discussion.

In the case of the striped bass (Figures 5 and 6), the results are somewhat different but can, I believe, be interpreted in a manner similar to the salmon. After exposure to 5 ppm benzene for 24 hours, the respiration rate of striped bass increased to a maximum. Here again, the attempt by the fish to increase their oxygen supply to metabolize the benzene is evident. The narcotic effect of the benzene appears at the 48 hour exposure period at 14 cm/sec and is greatest in fish held at 7 cm/sec after an exposure time of 72 hours. A gradual recovery from narcosis is apparently being achieved at the 96 hour exposure period at both current velocities. Striped bass exposed to 10 ppm benzene show an apparent narcosis within 24 hours (Fig. 6) and, as with the fish exposed to 5 ppm benzene, appear to be able to recover from this effect rather quickly, depending upon the current velocity. A reasonable hypothesis for the difference between the fish held at 7 and 14 cm/sec is the increased flushing rate at 14 cm/sec. Even though more benzene may be carried across the gill surface at the higher water velocity, so is more oxygen available, thus decreasing the effect of the benzene at 14 cm/sec.

The differences in response to benzene between the salmon and the striped bass may be due to several variables. The salmon were smaller than the bass, thus they had smaller gill surface. The benzene would diffuse into the blood and accumulate at a slower rate in the salmon, but would also be excreted at a slower rate. Differences in the amount of lipid-rich tissue in the two species could also have been a factor. Harper[17] found that in mammals the $NADPH_2$ involved in utilizing lipids and detoxifying ben-

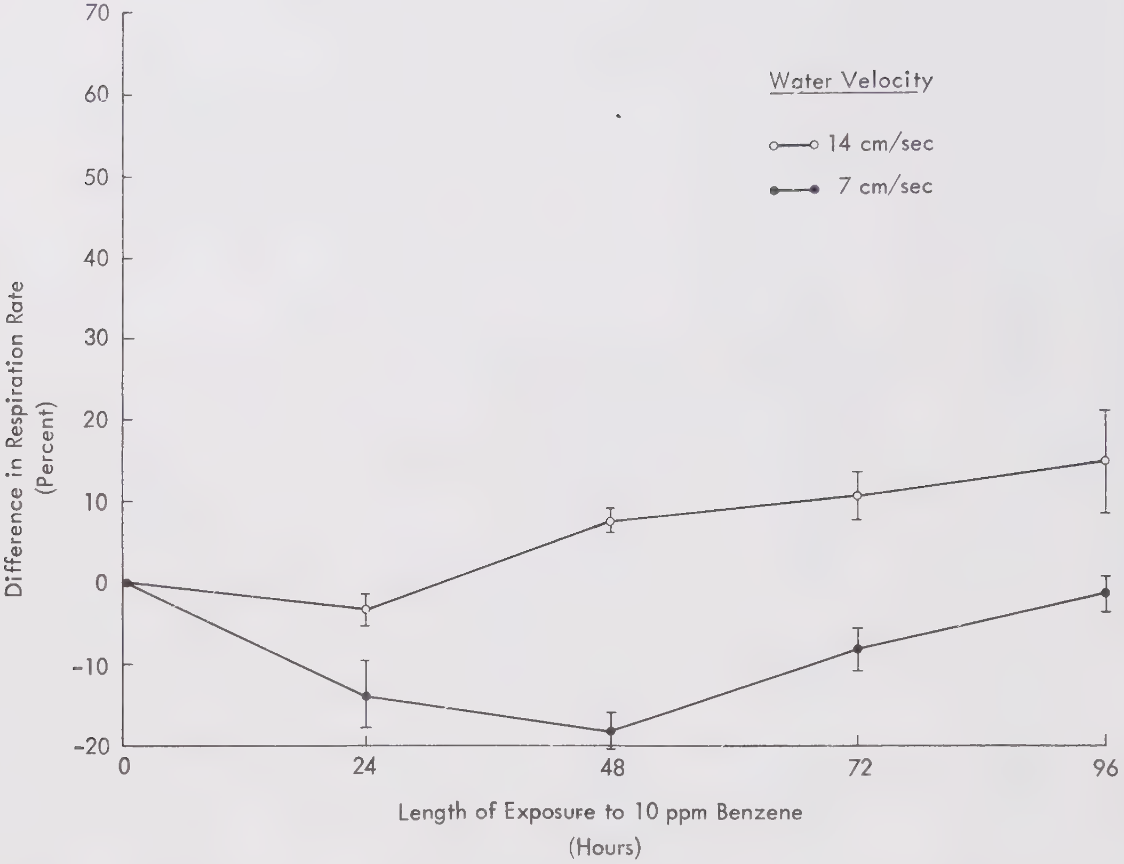

Figure 6: Relationship Between Percent Difference from Control Fish in Respiration of Juvenile Striped Bass Exposed to 10 ppm Benzene and Length of Exposure. Each Point Represents the Mean of 5 Fish with 2 Standard Errors Shown.

zene comes from the HMP shunt, part of the cycle for the catabolism of glucose. If a fish is not lipid-rich, the shunt ceases to operate and the incoming carbohydrate is changed directly to CO_2 and H_2O. The effect would be a lowering of the rate of detoxification and an increase in accumulation, thus a longer period of narcosis. Analyses of total body fat showed the salmon to have an average lipid content of 11 percent where the striped bass had a lipid content of 21 percent.

That narcosis exhibited by the fish used in these studies was reversible was demonstrated (Fig. 7). This is true for the exposure periods and the concentrations used. Investigation of potential effects of benzene on other life history stages of fishes, such as the egg and larval forms, which are not as mobile should be conducted.

Though the exposure tests in this experimentation were conducted under static conditions and extrapolation of laboratory results to the natural environment is difficult, potential effects were shown that under certain conditions could be hazardous to fish. Further investigation should be undertaken to elucidate the mechanisms of the responses to benzene and other water-soluble components of petroleum oil that can conceivably effect the production of aquatic species.

ACKNOWLEDGEMENTS

Special thanks are given to John Hiscox, Howard Bailey and Willard Johnson for their help in conducting these experiments. Mr. Richard Shomura and Drs. R. C. Averett and Jeanette Struhsaker reviewed the manuscript and their constructive criticisms are appreciated.

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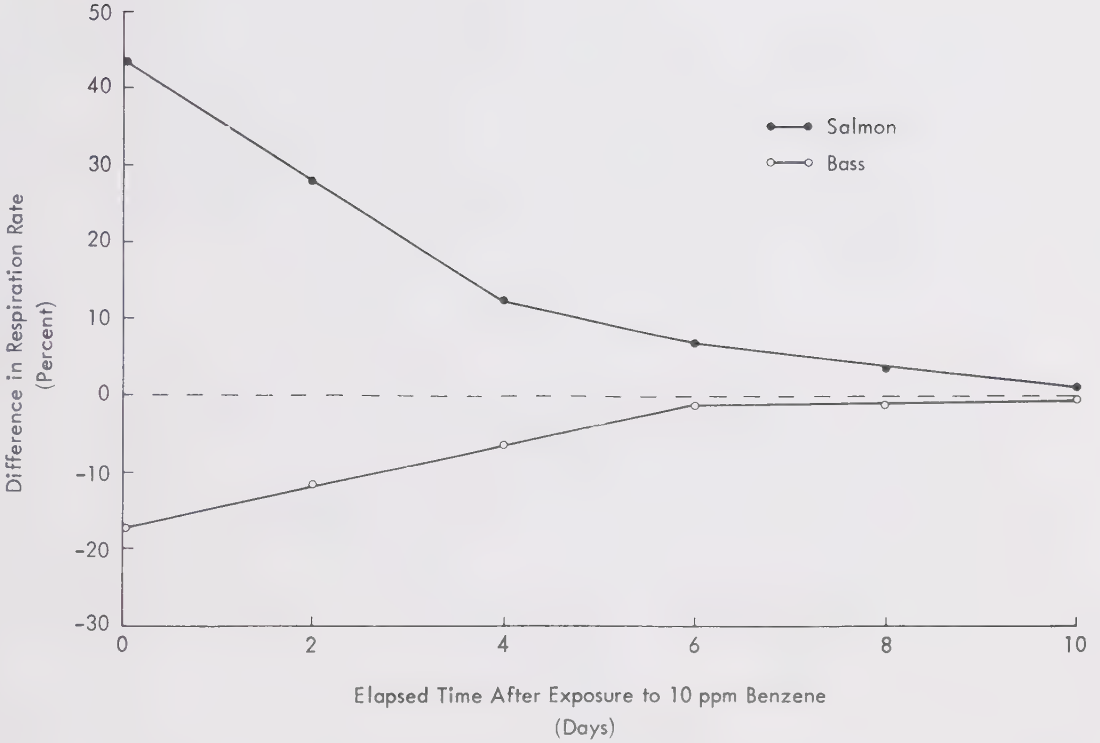

Figure 7: Relationship Between Percent Difference in Respiration from Control Fish of Juvenile Chinook Salmon and Striped Bass Exposed to 10 ppm Benzene for 24 Hours and Removed to Fresh Water. Each Point Represents the Mean Value for 5 Fish.

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HELMINTH PARASITES OF PORPOISES OF THE GENUS *STENELLA* IN THE EASTERN TROPICAL PACIFIC, WITH DESCRIPTIONS OF TWO NEW SPECIES: *MASTIGONEMA STENELLAE* GEN. ET SP. N. (NEMATODA: SPIRUROIDEA) AND *ZALOPHOTREMA PACIFICUM* SP. N. (TREMATODA: DIGENEA)

MURRAY D. DAILEY[1] AND WILLIAM F. PERRIN[2]

ABSTRACT

Parasite frequencies in 72 spotted porpoise, *Stenella graffmani* (Lönnberg, 1934), and 19 spinner porpoise, *S.* cf. *S. longirostris* (Gray, 1828), are reported and analyzed with respect to age of host. In addition to the new nematode *Mastigonema stenellae* gen. et sp. n. from the fore stomach of *S. graffmani* and the new fluke *Zalophotrema pacificum* sp. n. from the pancreatic duct of *S. graffmani* and *S.* cf. *S. longirostris*, parasites reported include *Anisakis simplex, Halocercus delphini, Crassicauda* sp., *Campula rochebruni, Tetrabothrium forsteri, Strobilocephalus triangularis, Phyllobothrium delphini*, and *Monorygma grimaldii*. Irreversible lesions in the ventral region of the skull due to infection of the air sinuses by a *Crassicauda*-like nematode were more frequent in skulls of calves of *S. graffmani* than in skulls of subadults and adults (129 specimens total), indicating that the parasite, or a condition correlated with its occurrence, is a significant factor in natural mortality of the spotted porpoise in the eastern tropical Pacific.

Porpoises of the genus *Stenella* are of great importance to the U.S. tropical tuna fishery (Perrin, 1969, 1970a). Yellowfin tuna associate with porpoise schools in the eastern Pacific, and the fishermen make use of this association in locating and capturing the tuna. Despite this economic importance, little is known of the ecology of the porpoises. Parasites have been previously reported from *Stenella longirostris, S. roseiventris, S. coeruleoalba, S. attenuata*, and *S. graffmani* (Dailey and Brownell, 1972). These reports have usually been from a small sample and did not include numbers of parasites per animal or percentage of sample infected. This report deals with two members of the genus in the eastern tropical Pacific: the spotted porpoise and the spinner porpoise. The taxonomy of the genus is currently in a chaotic state. Spinner porpoises from the eastern Pacific have been referred by recent authors to *Stenella microps* (Gray, 1846) and to *S. longirostris* (Gray, 1828)—Perrin and Hunter (1972). The spotted porpoise *S. graffmani* (Lönnberg, 1934) was described from Acapulco, but Rice and Scheffer (1968) recently referred all spotted porpoises to *S. dubia* (G. Cuvier, 1812), a decision that does not reflect a concensus of current opinion (Perrin, 1970b; Mitchell, 1970; Caldwell et al., 1971). We here refer the spotted porpoise examined to *S. graffmani* and the spinner porpoise tentatively to *S. longirostris.* The "eastern" and "whitebelly" spinner porpoises (Perrin, 1972) are considered to be geographical variants within one species and are not treated separately. This usage is provisional pending the results of current taxonomic investigations.

MATERIALS AND METHODS

We examined 72 specimens of *S. graffmani* and 19 of *S.* cf. *S. longirostris* (11 eastern and 8 whitebelly). These were collected during the course of investigations of morphology and reproduction. We collected parasites as we prepared skeletons of the animals for use

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as museum specimens. Capture data and museum numbers are presented in Appendix Tables 1 and 2. Also, we examined 67 skulls of spotted porpoise and 29 of spinner porpoise from museum collections, for bone damage caused by nematode infection. The museum specimens were from the eastern tropical Pacific and are listed below. Abbreviations used are: AMNH, American Museum of Natural History, New York; LACM, Los Angeles County Museum; SDMNH, San Diego Museum of Natural History; USNM, United States National Museum, Washington, D.C.

S. graffmani: AMNH130216, LACM27412, 27413, 27419, 27420, 27421, 27422, 27425, 27426, 27427, 27428, 27429, 27431, 27434, 31362, 31431; SDMNH20637, 21199; USNM-261427, 261428, 261429, 261430, 261431, 261432, 261433, 261434, 395264, 395265, 395266, 395267, 395268, 395615, 395616, 395617, 395618, 395926, 395927, 395928, 395929, 395935, 395936, 395937, 395938, 396027, 396029, 396034, 396037. The following LACM specimens, identified by field numbers, had no museum numbers when examined: GDF42, GDF57, MI563, RLB404, RLB500, WAW42, WAW51, WAW55. The following specimens, identified by field numbers are in the research collection at the Southwest Fisheries Center (SWFC below), La Jolla, Calif: CV160, JSL88, JSL89, JSL90, JSL95, RICE65-1, RICE66-3, WFP7, WPSG-01, WPSG02, WPSG03.

S. cf. *S. longirostris:* LACM27414, 27423, 27424, 27428, 27430, 27432, 27433; SDMNH-21200, 21427; USNM395269, 395270, 395271, 395272, 395273, 395274, 395275, 395930, 395931, 395932, 395933, 395934, 396030, 396032, 396035; LACM field numbers GDF56, RLB238, RLB405, WAW43, WAW50, WAW-52, WAW53, WAW54, WAW58, WAW60; SWFC field numbers CV240, CV241, CV245, RICE65-149, RICE67-102.

While rough-cleaning the porpoise carcasses for skeletal preparation, we examined the blubber, mesenteries, peritoneum, musculature, blowhole region, maxillary sinuses, mammary glands, and viscera (esophagus, stomachs, heart, lungs, liver, spleen, kidneys, gonads, intestine) for larval and adult parasites. We searched 3-m lengths of the intestine at the duodenal end, mid-length, and posterior end. Counts of cysts in the blubber should be considered as relative indices; we did not examine all the blubber carefully. We filled out a data form for each carcass indicating precisely which areas had been checked for parasites. All worms and cysts were fixed in Lavdowsky's (Formalin[3]-Acetic acid-Alcohol) or Bouin's fluid and stored in 70% ethanol. Cestode, trematode, and acanthocephalan whole mounts were stained with celestine blue B or Semichon's carmine. Specimens were sectioned singly or in situ at 6, 8, and 10 μ and stained with Mayer's hematoxylin and eosin Y or Mallory's trichrome. All material except nematode whole mounts were dehydrated in ethanol, cleared in xylene, and mounted in Piccolyte. Nematodes were cleared and mounted in glycerine. Drawings were made with the aid of a drawing tube. Measurements are given in millimeters unless otherwise stated. Average measurements are given with ranges in parentheses.

THE PARASITES

Counts of parasites collected are tabulated in Appendix Tables 1 and 2.

Nematoda

***Anisakis simplex* (Rudolphi, 1809, det. Krabbe, 1878)**

This nematode was the most frequent parasite collected during this study. The taxonomic criteria used in identification of these specimens were those presented by Davey (1971) in his revision of the genus *Anisakis*. *A. simplex* was found in the stomachs of both host species and represents a new host report for both *S. graffmani* and *S. longirostris*. Anisakids have been previously reported from other species of *Stenella* (Delyamure, 1955; Kagei et al., 1967; Zam, Caldwell, and Caldwell, 1971; Dailey and Brownell, 1972).

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[3] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Halocercus delphini Baylis and Daubney, 1925

This parasite has been reported previously from the genus *Stenella* by Zam et al. (1971). They found three of 17 *S. plagiodon* (Cope, 1866) taken off the Florida coast infected with *H. delphini*. This report represents a new host record from *S. graffmani* and *S. longirostris*. Infections occurred in bunches with the anterior ends of the parasites embedded in capsules found outside of the bronchial walls (Figure 1). The body of each parasite lies in the bronchiole oriented in an anterior direction, never towards the apex of the lobe, similar to the orientation described for *Skrjabinalius cryptocephalus* (see Delyamure, 1955).

Mastigonema stenellae gen. et sp. n. (Nematoda: Spiruridae)

This nematode is described from three female specimens taken from the forestomachs of two *S. graffmani* (both recovered prior to present study) and one *S. longirostris*.

Mastigonema gen. n. (Ascaropsinae)

Mouth with two unlobed lips. Cervical cuticle not inflated or flanged. Buccal capsule cylindrical, with few connecting, annular, thickenings. Esophagus long, not divided into anterior and posterior portions; valve of typical spiruroid form. Females prodelphic, ovaries post-esophageal. Vulva in middle third of body. Cuticle transversely striated. Oviparous. Parasites of Cetacea.

Mastigonema stenellae sp. n. (Figures 2-6)

With characters of the genus: body whip-shaped, with thin anterior and enlarged posterior portions. Stoma triangular; two large lips. Buccal capsule reinforced with connecting rings, cervical papillae present, eggs with enlarged cap.

Female: 25.5 (23.5-28.5) long by 1.2 in maximum width, 7.0 from posterior end. Buccal capsule 0.054 long, tapering from 0.045 wide at anterior to 0.032 at esophageal junction. Nerve ring 0.281 from anterior end, surrounding esophagus. Esophagus 8.5-11.7 long, widening at approximately 2.59 from anterior end. Ovaries directed anteriorly then reflexing sharply. Vulva muscular, 16.64 from anterior, vagina vera 0.13 long by 0.086 wide, vagina uterina 0.81 long by 0.11 wide. Eggs 0.034 long by 0.032 wide, with swollen cap slightly larger than bottom portion. Anal lip large, anus 0.22 from posterior tip. Tail conical with large mucron.

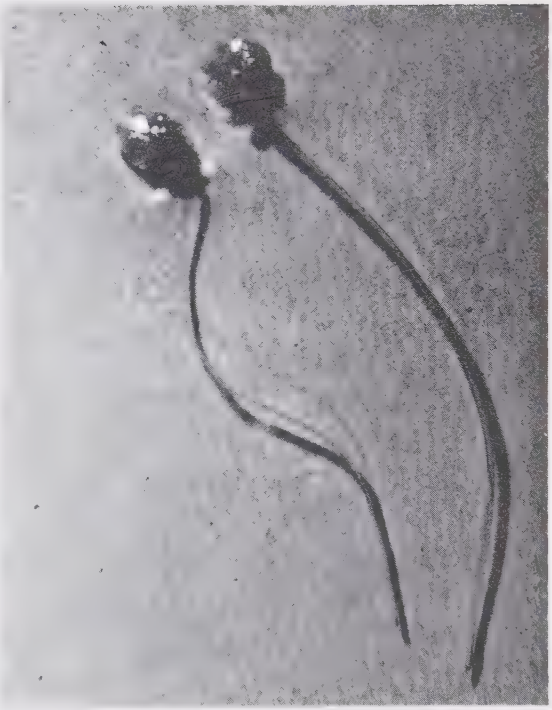
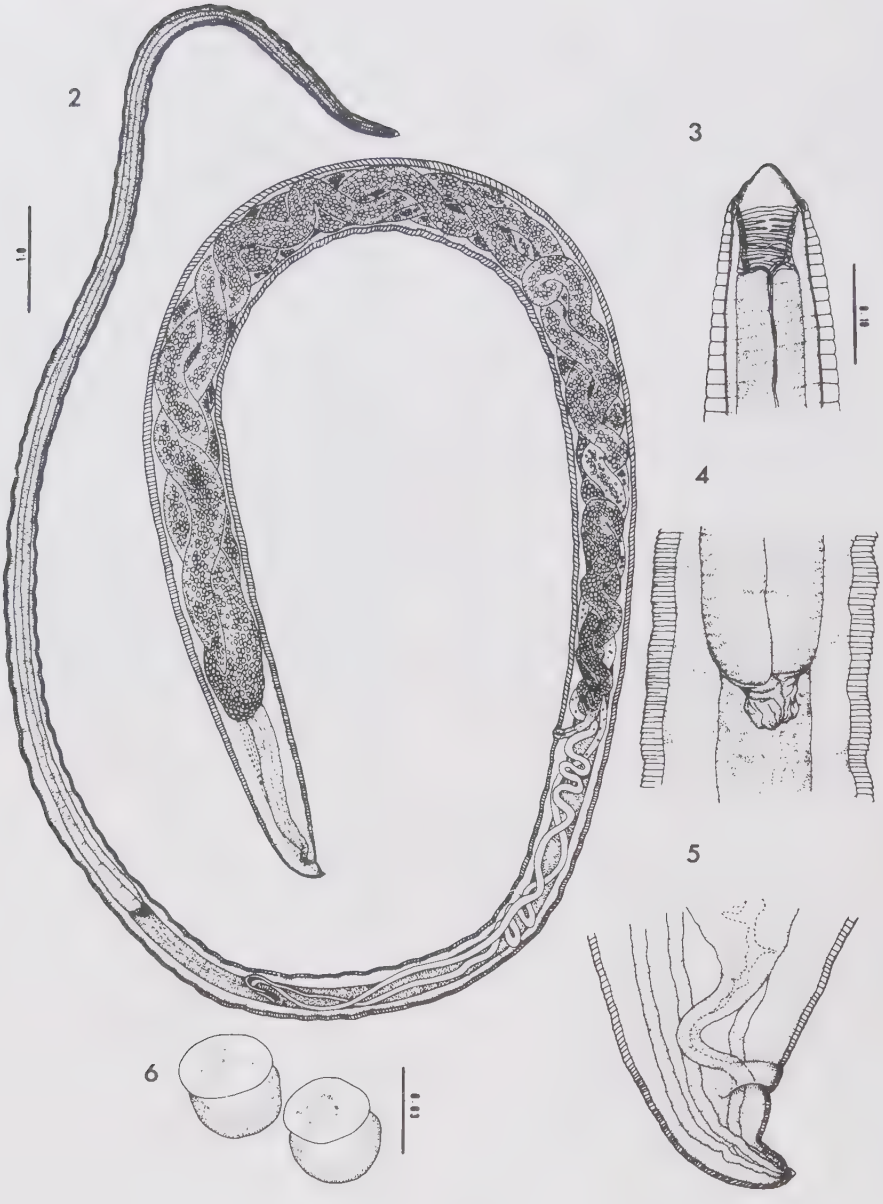


FIGURE 1.—*Halocercus delphini* with anterior end embedded in capsule. (X7)

Hosts: *Stenella graffmani*, *S. longirostris*.
Location: Forestomach.
Locality: Eastern tropical Pacific Ocean; holotype from *S. longirostris* collected at approximately lat 8°N, long 107°W.
Type specimens: USNM Helminth Collection holotype female No. 72159, paratype No. 72160.

Remarks: A search of the literature indicates this is the first report of a spirurid



FIGURES 2-6.—*Mastigonema stenellae* sp. n.: 2. Entire worm. 3. Cephalic region, showing annular thickenings. 4. Esophageal-intestinal valve. 5. Caudal region. 6. Eggs, showing enlarged caps.

nematode parasitizing a marine mammal. The general body shape of this nematode is similar to that seen in *Vasorhabdochona cablei* Martin and Zam, 1967, *Trichospirura leptostoma* Smith and Chitwood, 1967, and *Freitasia teixeirai* Baruš and Coy, 1965. However, the structure of lips and buccal capsule place it in the subfamily Ascaropsinae rather than with the rhabdochonids. Of the genera in this subfamily it most closely resembles the genus *Pereirai* Cuocolo, 1943. It differs from *Pereirai* in the following characteristics; lips are unlobed, cuticular flange is lacking, buccal capsule has few annular thickenings, esophagus not divided into anterior and posterior portions, and vulva in posterior half of body.

Crassicaudidae Skrjabin et Andrews, 1934

Crassicauda sp. A single infection of this tissue nematode was found in the 78 animals examined (1.3%). The worms were in the abdominal muscle adjacent to the mammary gland of *S. longirostris*. A large abdominal cyst was also found in the same area. Sections revealed large numbers of *Crassicauda* sp. eggs as well as portions of the female worm (Figure 7). Entire worms were not recovered so specific identification was not possible. However, egg

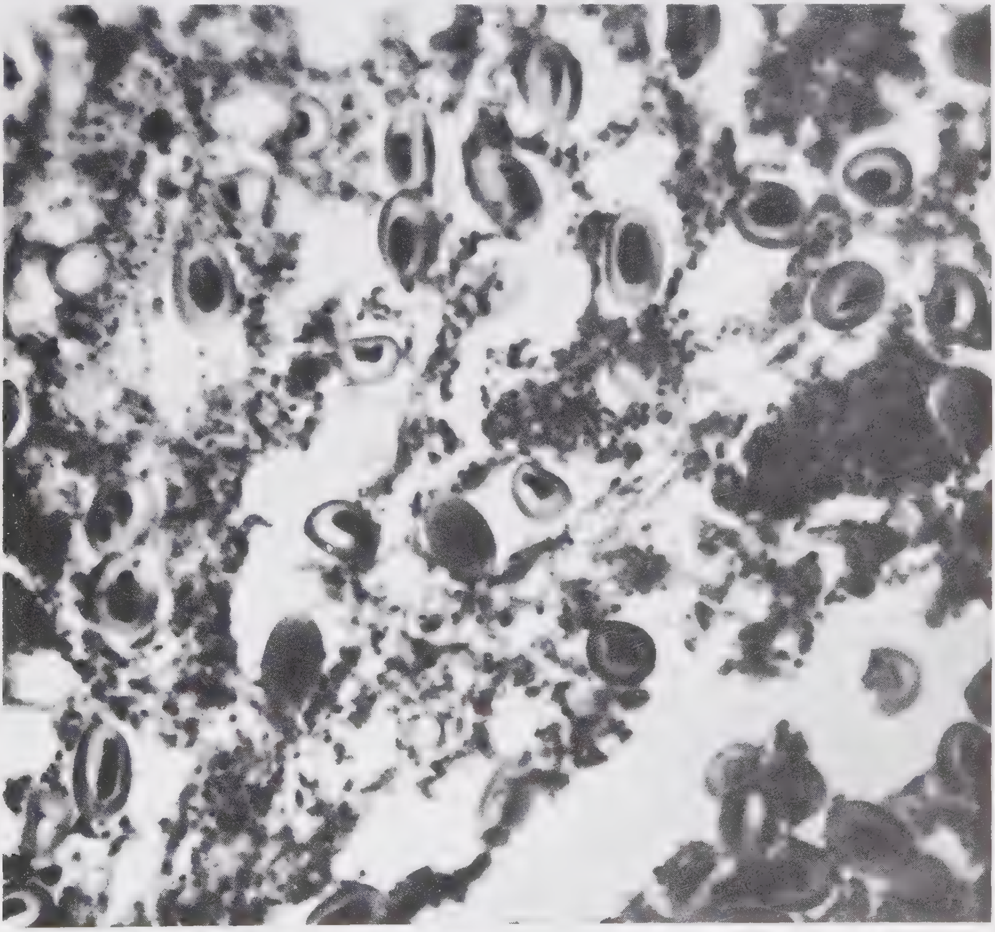


Figure 7.—Section through abdominal cyst with *Crassicauda* eggs. (X150)

measurements resemble those given for *C. grampicola* by Johnston and Mawson (1941) from Risso's porpoise, *Grampus griseus* (Cuvier, 1812), taken at New South Wales, Australia.

Another single specimen with *Crassicauda* affinities was recovered by James G. Mead, University of Chicago, Department of Anatomy, while dissecting the head of a *S. graffmani*. The worm was taken from the pterygoid air sinus. The pterygoid bone was eroded in the region in which the specimen was found. We assume that extensive bone damage found by us in other specimens we examined (Figure 8) was also caused by infestations of this nematode, although, judging from the published literature, the possibility cannot be dismissed that more than one species is involved. Reysenbach de Haan (1957) reported *Stenurus globicephalae* Baylis and Daubney, 1952, in the sinuses and cava tympani of the pilot whale, *Globicephala melaena* (Traill, 1809). Norris and Prescott (1961) collected "large quantities of a nematode (*Stenurus* sp.)" from the lateral air sinus of a dall porpoise, *Phocoenoides dalli* (True, 1885). Tomilin and Smyshlyayev (1968) reported that a "nematode *Stenurus minor* attacks the hearing organs of the Black Sea porpoise *Phocaena* and by clogging the cavity around the earbone may kill its host or severely complicate its existence." Brodie (1971) reported *Crassicauda* sp. as a middle ear parasite of the white whale, *Delphinapterus leucas* Pallas, 1776, in Cumberland Sound, Baffin Island. Yamada (1956) examined skulls of approximately 80 false killer whales, *Pseudorca crassidens*, from a stranded group of approximately 150 and found "basket-like" lesions in the pterygoid region of 40 skulls. He ascribed the damage to parasitic infection, "most probably by nematodes," and stated that such damage is a common occurrence in *Grampus* and *Globicephala* in Japanese waters.

Trematoda

The trematodes recovered during this study are represented by two genera known from marine mammals and three specimens of one genus that has been found in teleost hosts.

Zalophotrema pacificum sp. n.
(Figures 9 and 10)

Description: Based on measurements from 26 specimens. With characteristics of the genus. Body elongate. Dorsoventrally flattened, 10 mm (8.3-12.6) long by 1.7 mm (1.4-2.0) wide. Cuticle spinose. Oral sucker 535 μ (398-592) long by 575 μ (439-673) wide; opening slightly subterminal. Pharynx pyriform, 494 μ (398-541) long by 314 μ (255-367) wide. Intestinal cecum bifurcates immediately caudad to pharynx with each lateral branch dividing into short anterior and long posterior portions. Both anterior and posterior cecal branches contain numerous diverticula; anterior branch terminating lateral to posterior edge of oral sucker, posterior branch terminating near posterior end of body. Excretory pore terminal. Acetabulum 600 μ (520-710) in diameter, located approximately mid-body. Cirrus unarmed. Testes large, lobed, in tandem and extending posterior to equatorial third of body. Ovary pretesticular, lobed, 333 μ (235-418) long by 477 μ (310-765) wide. Mehlis's gland posterior and dorsal to ovary. Uterus coiled, preovarian. Genital pore just preacetabular. Vitellaria follicular, occupying entire anterior half of body from level of genital pore to shoulder region of ceca, extending posterior from genital pore in lateral bands to posterior end of body. Eggs, oblong, operculate, round in cross-section, mean measurements of 20 eggs, 61 μ long by 42 μ wide.

Hosts: *Stenella longirostris*, *Stenella graffmani*.

Location: Pancreatic duct.

Locality: Eastern tropical Pacific Ocean; holotype from *S. graffmani* collected at lat 12°5′N, long 93°18′W.

Type specimen: USNM Helm. Coll. No. 72158.

Remarks: Currently there are three species in the genus *Zalophotrema* (Stunkard and Alvey, 1929): *Z. hepaticum* Stunkard and Alvey, 1929, described from the bile ducts of a California sea lion, *Zalophus californianus* (Lesson, 1828), at the New York Aquarium; *Z. curilensis* Gubanov, 1952, from the bile ducts of

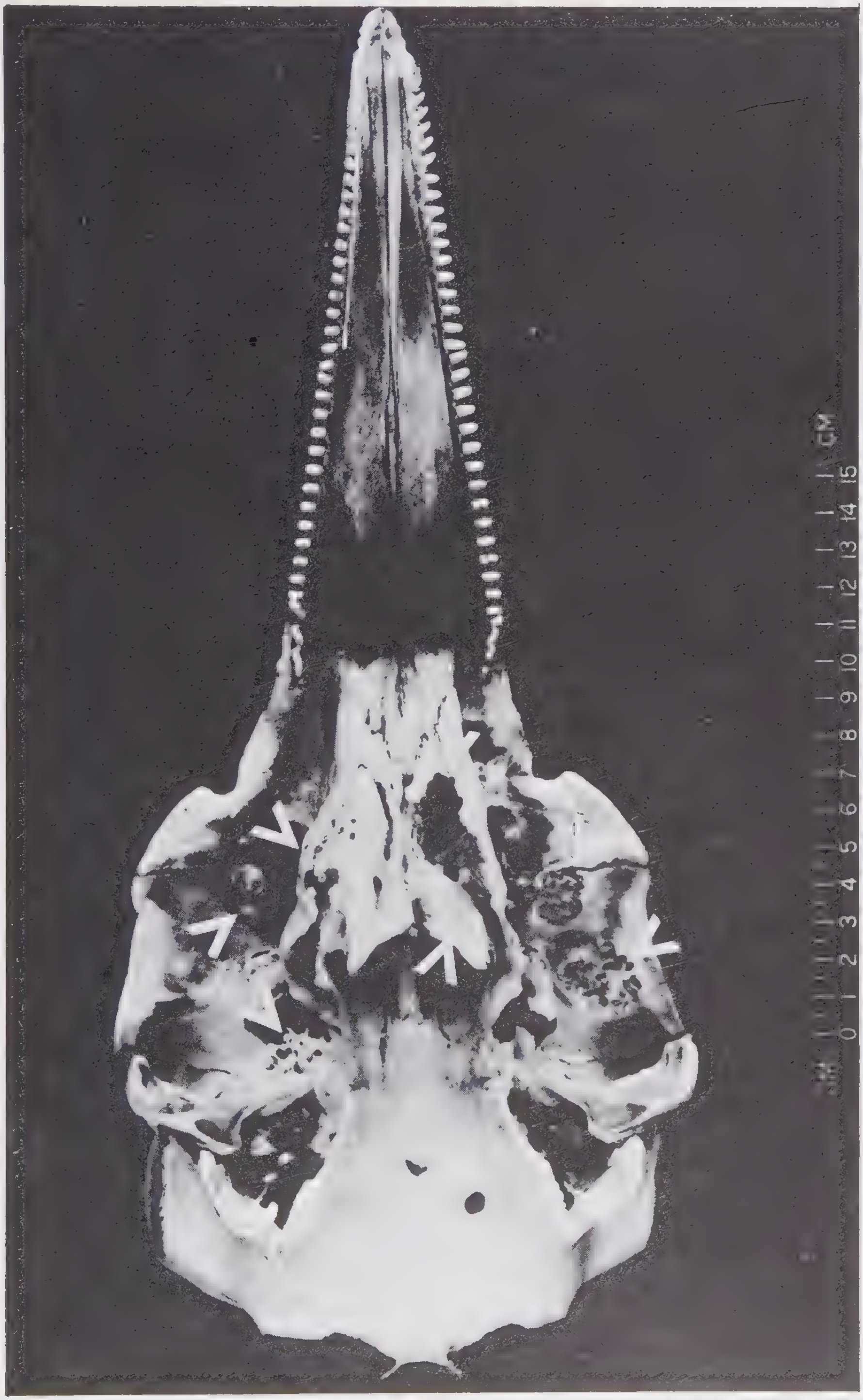

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FIGURE 8.—Ventral view of skull of spotted porpoise, *Stenella graffmani*, showing bone lesions (arrows).

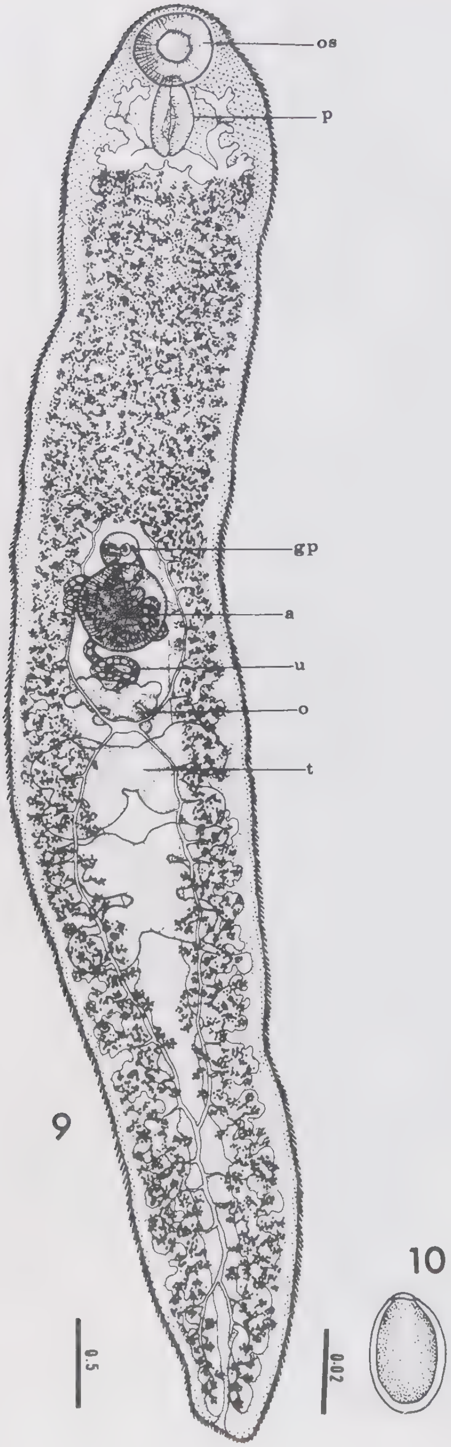
a sperm whale, *Physeter catodon* L; and *Z. lubimowi* Petrov and Chertkova, 1963, from the liver of a southern sea lion, *Otaria byronia* (Blainville, 1820) at the Moscow Zoo. *Zalophotrema pacificum* sp. n. can be easily separated from the three previously described species. *Z. lubimowi* differs from all other species in the genus in that it does not have confluent vitellarian fields anteriorly. *Z. curilensis* differs from *Z. pacificum* by larger body size (18-22.5 mm long by 5-7 mm wide) as well as the acetabulum being larger than the oral sucker. *Z. pacificum* sp. n. is most similar to *Z. hepaticum* in general body shape but differs in the following characteristics: body width (*Z. hepaticum* 3.0-3.6 mm wide), sucker ratio (in *Z. hepaticum* oral sucker almost twice as large as acetabulum while in *Z. pacificum* sp. n. suckers are approximately same size), ratio of distance between suckers to body length (*Z. hepaticum* 1:13, *Z. pacificum* sp. n. 1:2.5), distribution (percentage) of preacetabular vitellaria (*Z. hepaticum* nearly twice as large as those of Z. pacificum sp. n.), and egg size (75 μ long by 50 μ wide in *Z. hepaticum*).

Campula rochebruni (Poirier, 1886) Bittner et Sprehn, 1928

This parasite was recovered from the stomachs and hepatopancreatic ducts of three (two *S. graffmani* and one *S. longirostris*) of 78 (3.9%) animals examined. This is a new host record for this parasite and represents the first report from the genus *Stenella*. *C. rochebruni* was originally described from *Delphinus delphis* L. in European waters.

Incidental Trematodes

Three specimens of the genus *Hirudinella*



FIGURES 9-10.—*Zalophotrema pacificum* sp. n. 9. Entire worm, ventral view; 10. egg. Abbreviations used: a - acetabulum; gp - genital pore; o - ovary; os - oral sucker; p - pharynx; t - testis; u - uterus.

Garsin, 1730, were recovered from the forestomachs of three hosts (two *S. longirostris* and one *S. graffmani*). Members of this genus are commonly parasites of teleost fishes and were probably ingested with a meal of fish and not established parasites of these hosts.

Cestoda

Tetrabothrium forsteri (Krefft, 1871) Fuhrmann, 1904

This cestode was recovered from the intestine of over 50% of the examined hosts and occurred in both *S. graffmani* and *S. longirostris*. This is the first report of this parasite from either of these hosts. *T. forsteri* (Krefft, 1871) was first described by Krefft (1871) under the name of *Taenia forsteri* from *Delphinus delphis* L. (= *D. forsteri*) caught off the coast of New Zealand and later transferred to the genus *Tetrabothrium* by Fuhrmann (1904). A complete review of the literature on this species is given by Delyamure (1955).

Strobilocephalus triangularis (Diesing, 1850) Baer, 1932

This tetrabothriid has a complex taxonomic history that is covered by Delyamure (1955). The parasite apparently anchors its scolex in the colon wall when small and grows inside a fibrotic capsule formed by the host (Figures 11 and 12). This is the first report of this parasite from the genus *Stenella*. It has been reported from the Pacific Ocean by Baer (1955), who described material taken from an unidentified dolphin captured in the waters of the Marshall Islands. There are numerous reports of the parasite from Atlantic Ocean hosts (*Hyperoodon ampullatus*) (Forster, 1770) (= *H. rostratus*), *Mesoplodon bidens* (Sowerby, 1804), *Lagenorhynchus acutus* (Gray, 1828), *Steno bredanensis* Lesson, 1828 (= *S. frontatus*), *Delphinus* sp. (Delyamure, 1955).

Phyllobothrium delphini (Bosc, 1802) and *Monorygma grimaldii* (Moniez, 1881) Baylis, 1919

These larval cestodes were recovered from

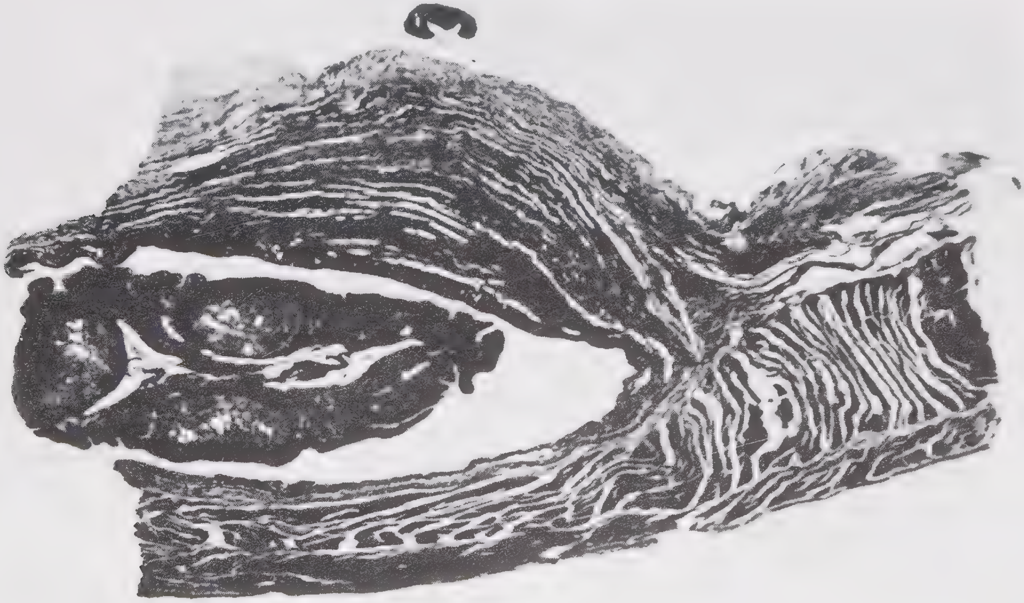


FIGURE 11.—Section through the capsule and scolex of *Strobilocephalus triangularis* from the rectum of *S. graffmani*. (X10.5)

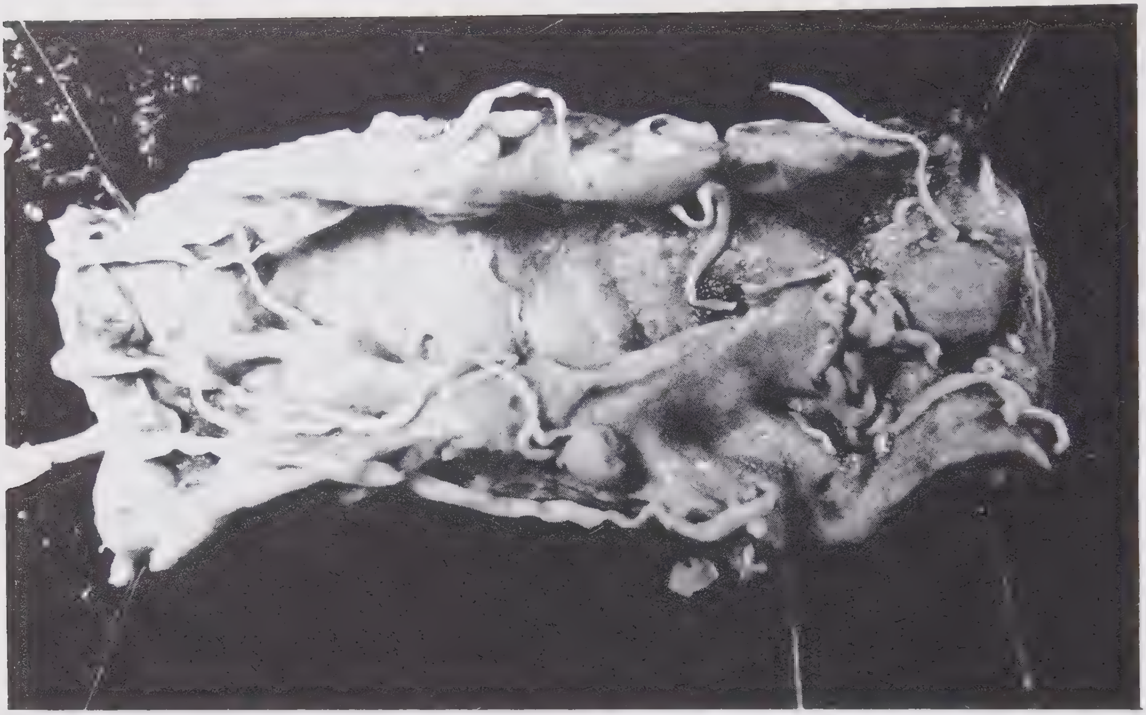


FIGURE 12.—*Strobilocephalus triangularis* attached in rectum of *Stenella graffmani*. (X1)

a large proportion of the animals examined. The history of these worms has been discussed by Delyamure (1955), Dollfus (1964), Williams (1968), and Dailey and Brownell (1972). *P. delphini* was always found in the blubber and *M. grimaldii* in the mesenteries.

PARASITE LOAD RELATIVE TO AGE OF HOST

The availability of data for a large sample of porpoise specimens, especially of *S. graffmani*, dissected in relatively uniform manner provides an unique opportunity to examine infection relative to age of the host for certain of the more frequently encountered parasite species. We discuss only the parasite species for which patterns of infestation are apparent in the data.

Spotted Porpoise, *Stenella graffmani*

The sample of *S. graffmani* examined may be divided into four age classes on the basis of total length, the developmental pattern categories defined by Perrin (1970b) and degree of sexual maturity (Figure 13). Females were classified as adult by the presence of corpora of ovulation in the ovaries and males by presence of spermatogenesis in the seminiferous tubules, as determined by histological examination. Sixty-one of the 72 specimens were collected during a 1-month period, and the first three modes probably represent discrete reproductive cohorts. Analysis below of parasitism relative to age is in terms of the four age classes, except as noted in the case of the *Crassicauda*-like nematode in the air sinuses.

The percent infection for *Anisakis* in *S. graffmani* shows increase with age of the host (Figure 14), but very large numbers of worms were found only in subadults, and the parasite number frequency distribution for that class is obviously skewed to the right. The inference to be drawn is that either some reduction in number of worms occurs in a heavily infected porpoise as it matures, due to the life cycle

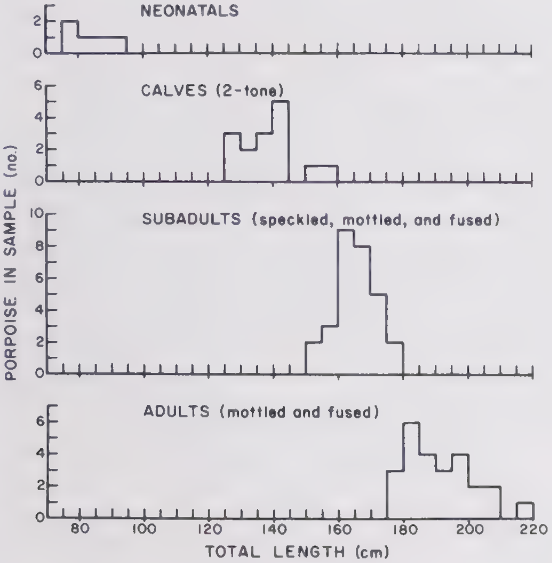


FIGURE 13.—Frequency distributions of total length, by age class, of spotted porpoise, *Stenella graffmani*, included in sample examined for parasites.

of the parasite and/or to possibly differential feeding habits of young and mature porpoise, or heavily infected individuals die before attaining maturity.

The case of the *Crassicauda*-like parasite in the air sinuses of *S. graffmani* certainly provides the most dramatic instance of infection varying with age. As stated above, the sinuses were not searched during dissection of most of the porpoise specimens, and only one specimen of the *Crassicauda*-type was recovered. Direct evidence, however, is provided of heavy infection by the areas of bone erosion on the lower surfaces of the skull (as illustrated in Figure 8). Given this circumstance, we expanded the series of porpoise specimens examined to include skeletal specimens in various museum collections. In all, 129 skulls of spotted porpoise from the eastern tropical Pacific were examined (see Materials and Methods). Since correlated data on size, reproductive condition, and color pattern were not available for most of the museum specimens examined, it was necessary to use other criteria of age for those specimens. The fetal and neonatal skulls examined were all from specimens we dissected. Those of the remaining skulls that were museum specimens were relegated to the three categories of calves, subadults, and adults by criteria of cranial features, using the sample of skulls from specimens we dissected to correlate these features with total length, sexual maturity, and color pattern. Museum skulls were assigned to the calf class when in condylobasal length, telescoping of facial elements, and closure of occipital sutures, they had not reached the adult condition. Skulls exhibiting adult length, telescoping, and occipital closure were divided into adults and subadults by the criterion of presence or absence of distal fusion of the premaxillary and maxillary bones of the rostrum. Rough correlation of the onset of fusion with attainment of sexual maturity was found among the skulls from specimens for which external data were also available (Table 1. Errors in classifying subadult skulls as adult and vice versa are approximately equal. Results of examination of the 129 skulls for bone damage (Table 2) demonstrate clearly that the rate of infection is very much higher in

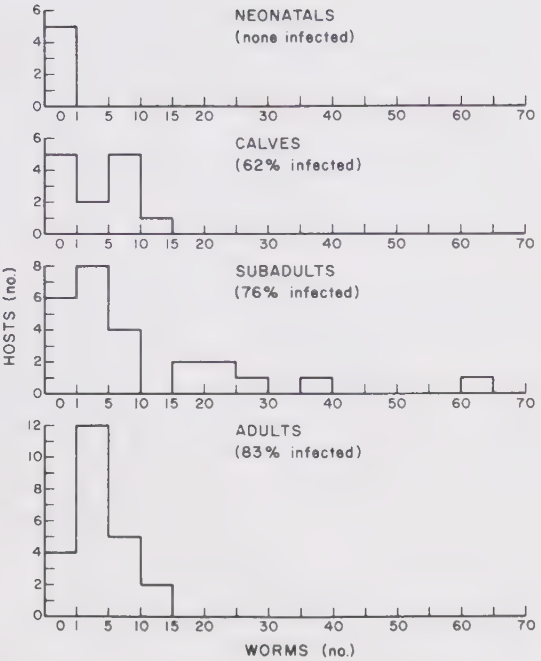


FIGURE 14.—Frequency distributions of levels of infection by *Anisakis* in four age classes of *Stenella graffmani*.

TABLE 1.—Incidence of distal fusion of pmx (premaxillary) and mx (maxillary) bones in specimens of *Stenella graffmani*.

Age class[1]	Examined	Pmx and mx fused	Error in classification
Subadults	31	6	19.4%
Adult	21	18	14.3%

[1] As determined by criterion of total length, color pattern, and sexual maturity.

TABLE 2.—Lesions of the ventral side of the skull in *Stenella graffmani*, presumably due to infection by a *Crassicauda*-like nematode.

Age class	Range of condylobasal length	Examined	Lesions present
	(mm)		
Nearterm fetuses and neonatals	209-236	10	0
Calves	302-359	18	8 (44.4%)
Subadults	356-446	45	5 (11.1%)
Adults	360-466	56	4 (7.1%)
Total		129	17 (13.2%)

calves than in subadults or adults. What is more, the most severely damaged skulls were those of calves. Such extensive damage is certainly irreversible, in that if repaired, traces would still be apparent in the form of bone callouses, depressions, or altered shape of bone elements. No such traces were found in any of the adult skulls examined, although we searched for them carefully. We conclude, therefore, that heavy damage is indicative of a probably morbid condition and that parasitism or a correlated condition is a significant factor in natural mortality of the spotted porpoise in the eastern tropical Pacific.

The patterns of infection relative to age by cysts of the cestodes *Monorygma* and *Phyllobothrium* (Figure 15) closely resemble each other, with little or no occurrence before subadulthood and 100% occurrence and greatest numbers in adults. As these are larval forms, the cysts presumably would have to be ingested by predators of the porpoise in order for the life cycles of the parasites to progress. Killer whales, *Orcinus orca*, have been observed by Perrin to prey on spotted porpoise, and sharks of several species have been observed to feed on dead and injured spotted porpoise during tuna fishing operations (Leatherwood, Perrin, Garvie, and La Grange, manuscript).[4] Killer whales and/or sharks are therefore possible candidates for terminal hosts of these two cestodes, although adult Tetraphyllidea have only been found in elasmobranchs. However, a life cycle involving a warm blooded intermediate host serving a cold blooded definitive host has not been previously demonstrated.

The two nonlarval cestodes, *Tetrabothrium forsteri* (Figure 16) and *Strobilocephalus triangularis* (Table 3), exhibit different patterns of occurrence, more like those of the nematodes, occurring with greatest numbers and frequencies in calves in the case of *T. forsteri* and in calves and subadults in the case of *S. triangularis*. This was especially striking for *S. triangularis*. In the two calves and two subadults with extremely heavy infections, the last meter of the intestine was all but blocked and swollen to three or four times its normal diameter. No adult examined was found to be infected with *S. triangularis*.

Spinner Porpoise, *Stenella* cf. *S. longirostris*

The smaller sample of spinner porpoise was divided into three age classes on the basis of length and sexual maturity, with subadults again defined as immature animals of adult size. Despite the small number of data for the spinner (Appendix Table 2), some differences are apparent between the patterns of infection for this species and for *S. graffmani*. For *Anisakis*, the specimen with the greatest number of worms (CV285) was a large adult female, which contrasts with the finding for *S. graffmani*, in which heaviest infections occurred in subadults. Bone erosion suggesting severe infection of the ventral air sinuses by a nematode was encountered in only 1 skull (of a subadult) of 53 examined. The parasite specimen was not recovered, precluding identification, but the damage was similar to that caused by the *Crassicauda*-like nematode in *S. graffmani*.

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[4] Leatherwood, J. S., W. F. Perrin, R. L. Garvie, and J. C. La Grange. Observations of sharks attacking porpoise (*Stenella* spp.). (Unpubl. manuscr.)

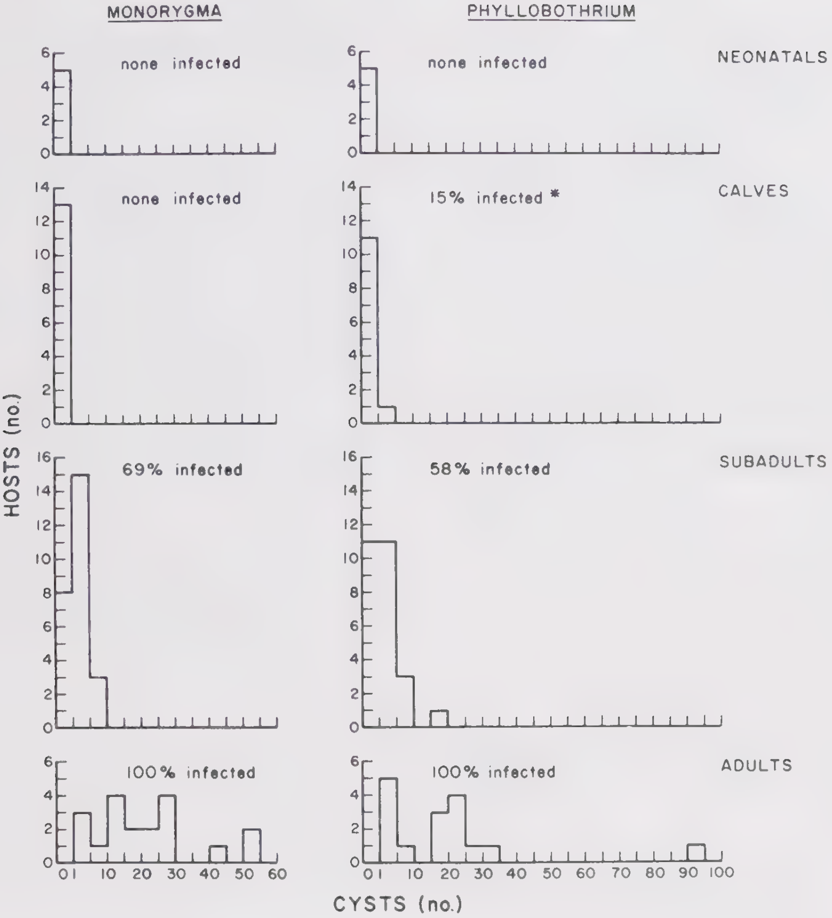

FIGURE 15.—Frequency distributions of levels of infection by cysts of *Monorygma grimaldii* and *Phylobothrium delphini* in four age classes of *Stenella graffmani*.

Infection by cestode cysts showed the same pattern as in *S. graffmani*, except that one adult specimen was found to be free of *Phyllobothrium* cysts. Also, as in *S. graffmani*, calves were most heavily infected with *T. forsteri*, and *Strobilocephalus triangularis* was encountered only in an immature specimen, a calf.

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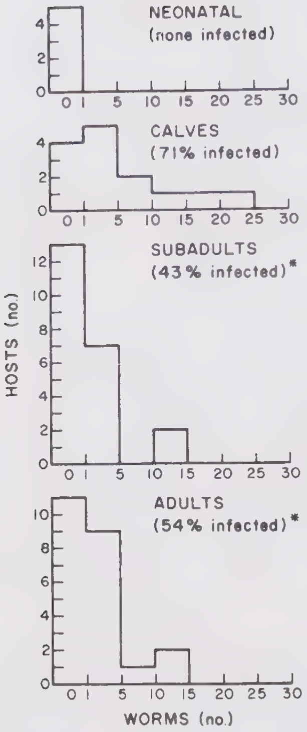

Figure 16.—Frequency distributions of levels of infection by *Tetrabothrium forsteri* in four age classes of *Stenella graffmani.*

Table 3.—*Strobilocephalus triangularis* in *Stenella graffmani.*

Age class	Examined	Infected
Neontals	5	0
Calves	14	3 (21.4%)
Subadults	26	3 (11.5%)
Adults	23	0
Total	68	6 (8.8%)

Los Angeles County Museum; Joseph R. Jehl, Jr., San Diego Museum of Natural History; and Charles O. Handley, Jr., U.S. National Museum, kindly made materials in their charge available for study.

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APPENDIX TABLE 1.—Parasites in *Stenella graffmani*.

Host						Parasites noted										
Field number	Museum number of skeletal specimen[1]	Collection number or locality[2]	Length (cm)	Sex	Age class[3]	*Anisakis simplex*	*Halocercus delphini*	*Mastigonema stenellae* sp. n.	*Zalophotrema pacificum* sp. n.	*Campula rochebruni*	*Tetrabothrium forsteri*	*Strobilocephalus triangularis*	*Phyllobothrium delphini*	*Monorygma grimaldii*	*Bolbosoma vasculosum*	*Bolbosoma balanae*
CV259	USNM395276	6	1,676	M	3	0	—	0	0	0	2	0	0	0	0	0
CV260	USNM395277	6	1,750	F	4	1	—	0	0	0	0	0	1	3	0	0
CV261	USNM395278	2	1,657	F	3	1	—	0	0	0	0	0	0	2	1	0
CV262	USNM395279	2	1,646	F	3	20	—	0	0	0	1	1	0	0	0	0
CV263	USNM395328	6	1,759	M	3	35	—	0	0	0	0	0	0	5	0	0
CV264	USNM395329	6	1,716	M	3	0	—	0	0	0	2	0	18	7	0	0
CV265	USNM395330	2	1,954	M	4	1	—	0	0	0	4	0	20	26	0	2
CV266	USNM395331	2	1,681	M	3	1	—	0	0	0	0	+	0	2	0	0
CV267	USNM395332	2	1,787	M	4	2		0	0	0	0	0	18	23	0	0
CV268	USNM395333	2	1,900	F	4	4	—	0	0	0	2	0	—	27	0	0
CV269	USNM395334	2	1,837	F	4	2	—	0	0	0	0	0	—	14	0	0
CV270	USNM395336	2	1,815	F	4	0	—	0	0	0	1	0	5	52	0	1
CV271	USNM395337	2	1,821	F	4	8	—	0	0	0	0	0	—	13	0	0
CV272	USNM395338	2	1,850	F	4	0	—	0	0	0	2	0	25	45	0	1
CV273	USNM395339	2	1,630	M	3	61	—	0	0	0	0	0	0	1	0	1
CV274	USNM395385	6	1,782	M	3	0	—	0	0	0	+	0	0	5	0	0
CV275	USNM395386	6	1,570	M	3	2	—	0	0	0	1	0	8	3	0	0
CV276	USNM395387	6	1,578	M	3	16	—	0	0	0	0	0	0	1	0	0
CV277	USNM395388	2	1,816	F	4	8	—	0	0	0	0	0	5	2	0	1
CV278	USNM395389	6	1,632	M	3	18	—	0	0	0	0	0	2	0	0	0
CV279	USNM395390	6	2,183	M	4	8	—	0	0	0	5	0	27	50	2	0
CV280	USNM395391	6	2,032	M	4	14		0	0	0	5	0	32	14	0	0

APPENDIX TABLE 1.—Parasites in *Stenella graffmani.*—*Continued.*

Host						Parasites noted										
Field number	Museum number of skeletal specimen[1]	Collection number or locality[2]	Length (cm)	Sex	Age class[3]	*Anisakis simplex*	*Halocercus delphini*	*Mastigonema stenellae* sp. n.	*Zalophotrema pacificum* sp. n.	*Campula rochebruni*	*Tetrabothrium forsteri*	*Strobilocephalus triangularis*	*Phyllobothrium delphini*	*Monorygma grimaldii*	*Bolbosoma vasculosum*	*Bolbosoma balanae*
CV281	USNM395392	6	1,739	F	3	27	—	0	0	0	+	0	1	1	0	0
CV282	USNM395393	6	1,740	F	3	2	—	0	0	0	2	0	6	4	0	0
CV283	USNM395394	6	2,021	M	4	5	—	0	0	0	13	0	90	28	0	0
CV284	USNM395395	2	1,927	F	4	0	—	0	0	0	0	0	—	—	0	1
CV286	USNM395397	2	1,647	M	3	0	—	0	0	100+	0	0	3	2	2	0
CV287	USNM395417	2	1,732	M	3	0	—	0	0	0	0	0	4	7	0	0
CV289	USNM395594	2	1,767	M	4	0	0	0	0	0	2	0	3	4	0	0
CV290	USNM395595	2	1,627	F	3	0	0	0	0	0	6	0	0	1	0	0
CV291	USNM395596	6	1,927	F	4	1	—	0	0	0	0	0	24	9	0	0
CV292	USNM395597	2	1,895	M	4	5	0	0	34	5	15	0	—	—	0	0
CV293	USNM395598	6	1,996	M	4	2	—	0	0	0	0	0	5	12	0	0
CV295	USNM395527	6	1,390	M	2	9	0	0	0	0	19	0	0	0	1	2
CV296	USNM395528	2	1,298	M	2	0	0	0	0	0	0	+	0	0	0	0
CV297	USNM395529	6	1,429	F	2	2	0	0	0	0	1	0	0	0	0	2
CV298	USNM395530	2	1,540	M	3	4	0	0	0	0	5	+	0	0	0	0
CV300	USNM395532	6	1,438	M	2	11	0	0	0	0	20+	0	0	0	2	2
CV303	USNM395535	6	1,433	M	2	0	0	0	0	0	4	0	0	0	0	0
CV304	USNM395458	2	862	M	1	0	0	0	0	0	0	0	0	0	0	0
CV305	USNM395459	2	780	F	1	0	0	0	0	0	0	0	0	0	0	0
CV306	USNM395460	6	913	M	1	0	0	0	0	0	0	0	0	0	0	0
CV307	USNM395461	2	803	F	1	0	0	0	0	0	0	0	0	0	0	0
CV308	USNM395466	6	793	F	1	0	0	0	0	0	0	0	0	0	0	0
CV309	USNM395463	6	1,878	F	4	9	0	0	0	0	9	0	21	26	0	0
CV310	USNM395464	2	1,801	M	4	3	0	0	0	0	1	0	21	17	0	0
CV311	USNM395465	6	1,995	M	4	4	0	0	0	0	3	0	18	23	0	0
CV312	USNM395462	2	1,640	F	3	7	0	0	0	0	0	0	1	0	0	0
CV313	USNM395467	2	1,601	M	3	8	0	0	0	0	5	0	0	2	0	0
CV314	USNM395468	2	1,842	F	4	1	0	0	0	0	0	0	+	+	0	0
CV315	USNM395603	2	1,621	M	3	7	+	0	0	0	12	0	3	5	0	0
CV316	USNM395604	2	1,679	M	3	12	0	0	0	0	0	0	1	4	0	0
CV317	USNM395605	2	1,375	M	2	7	0	0	0	0	5	0	0	0	0	2
CV318	USNM395606	2	1,444	F	2	8	0	0	0	0	0	0	0	0	0	0
CV319	USNM395607	6	1,681	F	3	2	0	0	0	0	1	0	5	0	0	0
CV320	USNM395608	2	1,670	M	3	20	+	0	0	0	13	0	7	0	0	0
CV321	USNM395609	2	1,525	M	3	1	0	0	0	0	0	0	1	0	0	0
CV322	USNM395610	6	1,423	F	2	9	0	0	0	0	6	0	0	0	0	0
CV323	USNM395611	2	1,617	M	3	5	0	0	0	0	0	0	4	2	0	0
CV324	USNM395612	6	1,356	F	2	0	0	0	0	0	13	0	+	0	0	0
CV325	USNM395613	6	1,348	M	2	4	+	0	0	0	8	0	1	0	2	2
PQ01	USNM395407	lat ~8°N, long 107°W	1,978	M	4	3	—	0	0	0	0	0	5	18	0	0
PQ02	USNM395408	lat ~8°N, long 107°W	1,590	M	2	7	—	0	0	0	0	+	0	0	0	0
[4]PQ04	USNM395410	lat ~8°N, long 107°W	1,677	F	3	3	—	0	0	0	0	0	2	8	1	0
WFP10	CAS15662	lat ~14°N, long 100°W	1,865	F	4	11	—	0	0	0	0	0	—	—	0	0
WFP11	UCMP86284	lat ~14°N, long 99-108°W	1,304	M	2	—	+	—	—	—	—	+	—	—	—	—
WFP12	MVZ140640	lat ~14°N, long 100°W	1,671	M	3	—		—	—	—	—	0	—	—	—	—
WFP13	UCMP23071	lat ~10°N, long 100°W	1,572	M	3	—	0	—	—	—	—	—	—	—	—	—
WFP19	CAS15663	lat ~10°N, long 100°W	1,536	M	3	—	0	—	—	—	—	—	—	—	—	—
WFP20	MVZ140643	lat ~10°N, long 100°W	1,708	F	3	—	0	—	—	—	—	—	—	—	—	—
WFP3	LACM37549	lat 14°30′N, long 99° 10′W	1,252	F	2	0	0	0	0	0	2	0	0	0	0	2
WFP4	LACM37550	lat 14°30′N, long 99° 10′W	1,260	M	2	0	0	0	0	0	0	0	0	0	0	0

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[1] CAS = California Academy of Sciences, San Francisco
LACM = Los Angeles County Museum
MVZ = Museum of Vertebrate Zoology, University of California, Berkeley
USNM = United States National Museum, Washington, D.C.

[2] Locality for collection number 2: lat 12°51′N, long 93° 18′W
Locality for collection number 6: lat 7°11′N, long 90°32′W

[3] 1 = near term fetus or neonatal
2 = calf
3 = subadult
4 = adult

[4] This specimen also infected with *Crassicauda.*

APPENDIX TABLE 2.—Parasites in *Stenella* cf. *S. longirostris*.

Host						Parasites noted										
Field number	Museum number of skeletal specimen[1]	Collection number or locality[2]	Length (cm)	Sex	Age class[3]	*Anisakis simplex*	*Halocercus delphini*	*Mastigonema stenellae* sp. n.	*Zalophotrema pacificum* sp. n.	*Campula rochebruni*	*Tetrabothrium forsteri*	*Strobilocephalus triangularis*	*Phyllbothrium delphini*	*Monorygma grimaldii*	*Bolbosoma vasculosum*	*Bolbosoma balanae*
CV285	USNM395396	2	1,769	F	4	56	—	0	50+	50+	3	0	27	13	2	0
CV288	USNM395593	6	1,726	F	4	2	—	0	—	—	—	—	+	+	—	—
CV294	USNM395526	6	1,494	F	2	1	+	0	0	0	10	0	8	0	1	0
CV299	USNM395531	2	1,189	M	2	4	0	0	0	0	5	0	0	0	0	4
CV301	USNM395533	2	1,396	F	2	0	0	0	0	0	0	0	0	0	2	0
CV302	USNM395534	2	1,184	M	2	9	0	0	0	0	20+	0	0	0	0	1
PQ03	USNM395409	lat ~8°N, long 107°W	1,571	F	3	8	0	0	0	0	8	0	8	2	2	6
PQ05	USNM395411	lat ~8°N, long 107°W	1,680	F	4	5	—	0	0	0	0	0	13	13	0	0
PQ06	USNM395412	lat ~8°N, long 107°W	1,729	F	4	9	—	1	0	0	0	0	0	4	1	0
PQ07	USNM395413	lat ~8°N, long 107°W	1,761	F	4	9	—	0	0	0	0	0	8	6	1	0
PQ08	USNM395414	lat ~8°N, long 107°W	1,734	M	4	1	—	0	0	0	2	0	7	17	0	0
PQ09	USNM395599	lat ~8°N, long 109°45′W	1,727	M	4	1	0	0	0	0	0	0	21	8	1	2
PQ10	USNM395600	lat ~8°N, long 107°W	1,086	F	2	7	—	0	0	0	0	0	0	0	0	1
PQ11	USNM395601	lat 8°N, long 109°45′W	1,054	F	2	0	—	0	0	0	6	+	0	0	0	1
WFP14	CAS15664	lat ~14°N, long 99-108°W	1,618	F	4	—	+	—	—	—	—	—	—	—	—	—
WFP15	CAS15665	lat ~14°N, long 100°W	1,637	M	4	—	+	—	—	—	—	—	—	—	—	—
WFP21	MVZ140641	lat ~14°N, long 100°W	1,651	M	3	—	+	—	—	—	—	—	—	—	—	—
WFP22	CAS15668	lat ~10°N, long 100°W	1,750	M	4	—	—	—	—	—	—	—	—	—	—	—
WFP6	LACM37551	lat 10°40′N, long 108°40′W	896	F	2	0	0	0	0	0	0	0	0	0	0	0

[1] CAS = California Academy of Sciences, San Francisco
LACM = Los Angeles County Museum
MVZ = Museum of Vertebrate Zoology, University of California, Berkeley
USNM = United States National Museum, Washington, D.C.

[2] Locality for collection number 2: lat 12°51′N, long 93°18′W
Locality for collection number 6: lat 7°11′N, long 90°32′W

[3] 1 = near term fetus or neonatal
2 = calf
3 = subadult
4 = adult

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New records of *Sargassum hawaiiensis* Doty and Newhouse (Sargassaceae, Phaeophyta), a deep water species

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Sargassum hawaiiensis Doty and Newhouse was described in 1966 from a fragmentation specimen dredged from a depth of 50 m off Oahu, Hawaii. Unitl recently, no further collections have been available for study. In 1968 and 1971 new material was collected from Penguin Banks off Molokai, Hawaii, during shrimp trawling operations by the National Marine Fisheries Service vessel "Townsend Cromwell". The specimens were obtained from depths of 183 and 200 meters.

A complete description of the species is given, which differentiates it from the three other species of *Sargassum* recognized from Hawaii. *Sargassum hawaiiensis* is distinguished by a combination of characteristics, these being: simple spines on some branches, terete vesicle petioles, muticous and spherical vesicles and bifurcate receptacles with narrow sterile bridges.

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Introduction

Three species of *Sargassum* are commonly encountered in Hawaii, *i.e., S. echinocarpum,* J. Ag., *S. obtusifolium* J. Ag., and *S. polyphyllum* J. Agardh. A fourth species, *S. piluliferum* C. Ag., is reported (Howe, 1934) only from Pearl and Hermes Reef, at the northwestern end of the Hawaiian chain. A fifth species, *S. hawaiiensis* Doty and Newhouse, has recently (Doty and Newhouse, 1966) been described from fragmentary dredged material. New collections from 183 and 200 m have now enabled a more complete description to be given of *S. hawaiiensis,* the subject of this paper.

A number of other species have been attributed to the Hawaiian Islands over the years but are now considered to be either misidentifications or synonymous with the previously described forms. Thus, *S. densum* Dickie (Dickie, 1877) is considered a synonym (Grunow, 1916) of *S. polyphyllum. Sargassum cymosum* C. Ag. has been attributed to Hawaii by Tilden (1902) and Chamberlain (1881), but the name appears to have been applied to what is recognized in Hawaii as *S. obtusifolium*. From the available descriptions, *S. cymosum* and *S. obtusifolium* appear to be Atlantic and Pacific forms of the same species, but until types and field collections can be compared no decision can be made as to their relationship.

The entire genus *Sargassum* is in need of a monographic treatment based on studies of the type collections and on plants in nature. In view of the over 250 species attributed to the genus, such a work will undoubtedly be a long time in coming. Recent critical evaluations of selected species of the genus by Womersley (1954) and Womersley and Bailey (1970) have resulted in a number of species being placed in synonymy. Studies underway by the first author (R. DeW.) also suggest that a number of Pacific species of *Sargassum* have been described from insufficient material. As a consequence, the high degree of variation of members of the genus has not been fully taken into account, resulting in the description of forms as species.

Although we recognize this problem, we believe that *Sargassum hawaiiensis* Doty and Newhouse should be reconfirmed in the literature and more completely described from the new, more complete material recently collected. The species was described from thalli dredged from a depth of 50 m off Kaneohe

Bay, Oahu, Hawaii, near Lat. 21° 31.3′ N, Long. 157° 48.3′ West. New collections consist of a number of complete and attached thalli which are fertile and have all structures needed for a critical evaluation of the species.

A number of authors (Reinbold, 1913; Setchell, 1936) have pointed out that the sex of the thallus may determine receptacle morphology in some species. The original description does not include data on the presence or absence of oogonia and/or spermatangia within the receptacles. The material now available has enabled us to obtain this information. In view of the scarcity of previous collections (one only), the fragmentary nature of the Holotype and the uniqueness of the habitat, *i.e.,* from 50–200 m, it seems worthwhile to elaborate on the original description of *S. hawaiiensis.*

Sargassum hawaiiensis

The present thalli of *S. hawaiiensis* were obtained by the second author (E.C.J.) while bottom trawling for shrimp. They were obtained at 183 m on May 4, 1968, at station 21, during cruise 36 of the "Townsend Cromwell". The trawling track ran along a course of 21° 09.7′ N from 157° 24.8′ W Long. to 157° 37.0′ W Long. Additional collections were made on September 23, 1971, at 200 m, on the "Townsend Cromwell" cruise 54, at station six. This trawl track ran from Lat. 21° 10.0′ N and Long. 157° 30.0′ W, to Lat. 21° 09.8′ N and Long. 157° 29.5′ West. A number of thalli were collected whole, with holdfasts attached to the shell fragments of a bivalve mollusc *Atrina sp*. The material was preserved in formalin. Exsiccata specimens of this material have been deposited in the herbariums of the Smithsonian Institution, Washington, D.C., the B. P. Bishop Museum, Honolulu, Hawaii, and in the herbarium of M. S. Doty, University of Hawaii, Honolulu, Hawaii.

The ecology of *S. hawaiiensis* and the other algae collected in the trawling hauls will be the subject of a later paper. What follows is a comparison of the newly collected material with the only previous collection, the Holotype specimen numbered *"M. S. D. 19134"* deposited in the B. P. Bishop Museum in Honolulu, Hawaii.

LEAF FORM

The newly collected material varies in height from 120–650 mm, with leaves (Fig. 1) up to 60 mm long and 10 mm wide. Leaf margins are irregularly dentate or here and there entire. A midrib is present and extends to just below the apex. The leaf apex is obtuse to irregularly indented. Cryptostomata are scattered over the surface. Leaves tend to be sessile. These features are as described for the Holotype.

One notable variation of the newly collected material from the Holotype is the absence of the furcate leaves illustrated by Doty and Newhouse. The new material, as illustrated in Figure 1, shows one incipient furcation. Such an absence of furcate leaves is not unknown in species of *Sargassum* described as possessing them. Similarly, *Sargassum obtusifolium,* also from Hawaii, can be found with or without such furcate leaves. Causes of this variation in leaf morphology are not known.

HOLDFAST, STEM AND BRANCH FORM

The holdfast of the new material is smooth, disc-shaped and often furrowed. The stem arises from the holdfast, varying in length from 20–50 mm, with primary branches arising predominantly from its apex. Such branches also arise from lower portions of the stem, but these are lost as the alga matures and their points of origin give rise to the bumpy appearance of the stem.

The stem is verrucose and more or less circular in cross-section. The branches are also

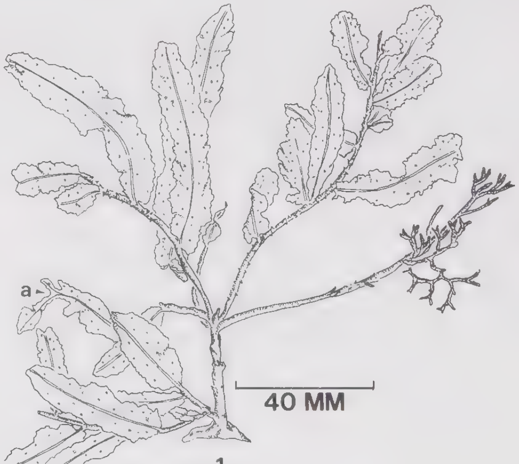

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FIG. 1. Habit sketch of *Sargassum hawaiiensis; note* the simple spines on some of the branches and the single leaf bifurcation (*a*).

circular in cross-section and some show the prickles described for the Holotype material. These prickles, more descriptively termed simple spines to distinguish them from the more complex, often furcate, spines of *Sargassum polyphyllum,* are loosely distributed over some of the branches. The origin of the simple spines is not clear, as their position suggests that they are not remnants of either receptacles or branches. The appearance and position of the complex spines alluded to above suggests that some at least may be remnants of vesicles that have sloughed off.

A number of branches show some degree of flattening toward the apex, a feature not mentioned in the original description. Where flattening occurs, it is often accompanied by a twisting of the branch.

VESICLE AND VESICLE PETIOLES

As with the Holotype material, vesicles are closely associated with the fertile branches. The vesicles are spherical, from 3–7 mm in diameter, smooth, muticous, and without any teeth or wings. The vesicle petiole is terete and about as long as the vesicles. The above agrees closely with the Holotype material.

RECEPTACLES

The receptacles of the Holotype material are described (Doty and Newhouse, 1966) as forming a loose cluster of cylindrical branches 0.2–0.3 mm in diameter when dry, with individual branch segments at times slightly exceeding 10 mm in length. In addition, the receptacular clusters are described as devoid of leaves and located apically. The newly collected material includes one specimen (Fig. 1) with the receptacular cluster likewise devoid of leaves, but other specimens (Fig. 2) show the more usual position for such clusters, *i.e.,* in the axils of leaves. Formalin and sea water preserved material indicates the receptacles to have diameters of 1 mm.

A number of other features concerning the receptacles should be noted. As illustrated in Figure 2, it is common for the receptacles to show a more or less dichotomous branching which extends even to their apices. This feature was also observed in the Holotype material. Also distinctive, is the narrow sterile bridge found between the fertile portions of the receptacles. No determination of sex was made on the Holotype material, but examination of the new material shows the majority to have both oogonia and antheridia present in the same receptacle. All receptacles show an identical morphology. There appears to be no sexual differentiation of thalli in this species.

Although the preserved material included no germling stages of *Sargassum hawaiiensis,* the presence of both spermatangia and oogonia on individuals collected from 183 to 200 m suggests that the species may reproduce at these depths. Of course, it is not known whether the reproductive bodies were viable before preservation.

Conclusions

Sargassum hawaiiensis may prove to be unique within the genus in its depth of occurrence. Since the plasticity of the genus with variation in environment is not well known (though it appears to be considerable), the species may be the modified offspring of a fertilized egg of one of the inshore species which drifted into deep water. Further studies may also indicate that currents are sweeping the material down from a shallower depth. How-

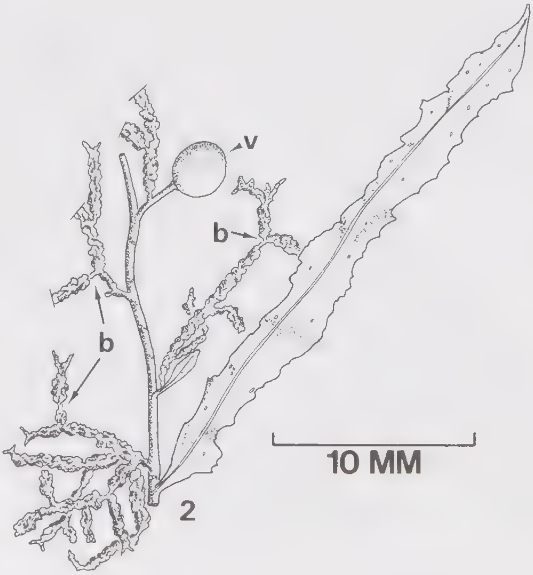

FIG. 2. Portion of a primary branch of *Sargassum hawaiiensis* showing receptacles with narrow sterile bridges (*b*) and bifurcate growth habit, a spherical and muticous vesicle (*v*), and the general leaf morphology.

ever, the fact that the thalli are attached, fertile, and to all appearances healthy, indicates that the alga can survive and possibly grow at 200 m.

Regardless of the depth range of reproducing individuals, *S. hawaiiensis* is a distinct species, as that term is understood and currently put into practice with the algae. As is the case with the other species of *Sargassum*, no single feature can be used to differentiate them. For *S. hawaiiensis* the combination of simple spines loosely scattered over some of the branches, the terete vesicle petioles, muticous vesicles, elongated, lax and bifurcate receptacles with sterile bridges, and the general leaf morphology differentiate this species from all others known.

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7306

LONG-TERM OLFACTORY "MEMORY" IN COHO SALMON, *ONCORHYNCHUS KISUTCH*[1]

Many experiments have correlated the importance of olfaction and the precise homing of sexually mature salmon. As juveniles, the fish are presumably imprinted on the natural odors of their natal-area water (Hasler, 1966). The odors apparently serve as cues to guide the adult's return. Thus, some type of "odor memory" must persist from the time of the downstream journey of the smolt to the return of the sexually mature adult. For introduced Lake Michigan coho salmon, *Oncorhynchus kisutch*, this is either ½ year (precocious males) or 1½ years.

The existence of long-term olfactory memory persisting over this time period has only been inferred. Idler et al. (1961) and Fagerlund et al. (1963) found that already homed salmon made unconditioned behavioral responses to home water. Hara, Ueda, and Gorbman (1965), Ueda, Hara, and Gorbman (1967), and Oshima, Hahn, and Gorbman (1969a) found specific EEG (electroencephalographic) responses to home-stream water. Hara (1970) in his review of this EEG technique states: "This electric response [from the olfactory bulbs] is specific in the sense that it cannot be evoked by water from spawning sites of other groups of breeding salmon." The EEG and behavioral studies strongly suggest long-term memory of the juvenile's stream experience. However, since these workers used homed adults that had recently experienced home water, the data are evidence only of an odor memory lasting from the time of removal from the home stream to the time of testing.

We tested coho salmon that were exposed to a synthetic odoriferous substance for 1 month during smoltification and then removed from any conceivable influence of this substance for 10 months. Ten months later these fish and controls were examined for olfactory bulbar EEG responses (after Hara et al., 1965) to the imprinting substance.

Materials and Methods

On 7 April 1970, approximately 2,500 hatchery-raised coho salmon smolts (1½ years old) were put into each of two contiguous 25-m sections of a raceway at a Wisconsin State fish hatchery at Crystal Springs. We marked the fish to eventually distinguish the upper section control subjects from the lower section experimentals. A small drop (⅓ m) prevented water in the lower section from reentering the upper section. Immediately below the drop a dilute concentration of morpholine was introduced by infusion pump at a rate to maintain a steady-rate concentration of 10^{-5} ppm. This value is one order of magnitude above an avoidance threshold of unconditioned coho salmon fingerlings (Wisby, 1952). On 5 May 1970, 1 month after initiation of the morpholine treatment, all but 50 fish from each raceway section were trucked to Lake Michigan and released as part of another experiment. The 100 remaining fish were moved to a hatchery near Madison, Wis., and held together in a single outside raceway for 10 months prior to EEG tests.

Our testing procedure was generally similar to that used by Hara et al. (1965) to examine olfactory bulb responses to home-stream water. The subject was paralyzed with gallamine triethiodide (2 mg/kg), restrained, and the gills perfused with tap water. One of the olfactory bulbs was exposed, and an electrode (Transidyne General, model 415[2]) was placed on the surface near the rear margin. The responses evoked by perfusion of the ipsilateral naris were amplified (Bioelectric Instruments, model DS2c) and recorded on a two-channel oscillograph (Hewlett Packard, model 7712B) for later analysis. This oscillograph was equipped with an integrating preamplifier for efficient quantification of bulbar activity. Therefore, all responses reported later are expressed as the sum of the positive areas under the response wave form.

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[1] This work was completed under financial support from the National Science Foundation (Grant No. GB 7616X) to Prof. Hasler and the University of Wisconsin Sea Grant Program which is a part of the National Sea Grant Program maintained by the National Oceanic and Atmospheric Administration of the U.S. Department of Commerce.

[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Beginning on 25 February 1971, one fish was examined per day with 1% and 0.01% morpholine stimuli. Fourteen fish were used. Each test was started at approximately 1000 hr. Every subject was tested with the morpholine concentrations and the responses compared with responses to 0.06 N NaCl. Stimuli were randomly ordered and presented for 10 sec followed by 75 sec of tap water rinse. The stimulus series was then repeated seven times.

Results

Fish that had been exposed to 10^{-5} ppm of morpholine as smolting juveniles evidenced significantly higher bulbar EEG activity over controls when tested with 1% and 0.01% concentrations of morpholine (Table 1). Responses to 1% morpholine gave a Mann-Whitney value of $U = 5$ (Siegel, 1956) with probability of 0.006 that the control group and the experimental group were drawn from the same treatment population. Responses to the 0.01% level were less markedly, but still significantly, different ($U = 11$, $P = 0.049$).

Discussion

Exposure to low concentrations of morpholine produced a sensitization which lasted at least 10 months. But, we did not attempt to determine whether this observed sensitization was exclusively to morpholine or to other stimulatory products. Casual observation of our data did not reveal the experimental subjects to be more responsive to NaCl than the controls; but this comparison was difficult to make in our experimental design because of the changing relationship between response amplitudes and background activity levels. (Hence, the necessity of continual comparison of morpholine response with NaCl response, our reference.) Even if overall olfactory responsiveness is increased as a result of pretreatment, sensitization to morpholine is still proportionally greater (experimental vs. control) 10 months later. We hypothesize that exposure to morpholine imprinted the fish during one of the critical periods in the life of the coho salmon, a period when the fish is undergoing physiological changes in preparation for entering a marine environment.

Independent evidence indicates the existence of a critical period. The Wisconsin Department of Natural Resources allows approximately 1 month of imprinting during the period of smoltification before releasing the fish into the river system. Imprinting for less time or at different stages of the life cycle seems to result in more straying (Peck, 1970).

Morpholine was chosen as the imprinting substance since the responses of fingerling coho salmon to it have been investigated (Wisby, 1952). Consequently, the concentration could be chosen with knowledge of the performance parameters of the coho salmon. It was necessary to be above threshold but not so high as to cause enthusiastic avoidance or sublethal damage. Because of the vagaries of the flow measurements

TABLE 1.—Morpholine-elicited EEG responses of morpholine-imprinted coho salmon compared with those of controls. E designated subjects were imprinted with morpholine at a concentration of 10^{-5} ppm; C designated were controls. Median EEG responses of each fish to 1% morpholine and 0.01% morpholine stimuli are ranked (ties carry averaged ranks) and Mann-Whitney U values and probability values are shown for each treatment level.

1%														
Group	C	C	C	C	C	C	E	E	E	E	E	C	E	E
Median[1]	63.5	100	140	220.5	230	250	255	266.5	287	333	351.5	600	915	917
Rank	1	2	3	4	5	6	7	8	9	10	11	12	13	14
						$U = 5$	$P = 0.006$							
0.01%														
Group	C	C	E	C	C	C	E	E	C	E	E	C	E	E
Median[1]	0	0	0	0	0	25.6	38.5	41.5	45	45	50	50	67	77.5
Rank	3	3	3	3	3	6	7	8	9.5	9.5	11.5	11.5	13	14
						$U = 11$	$P = 0.049$							

[1] Median response = $\left(\frac{\text{response morpholine}}{\text{response 0.06 N NaCl}} \times 100\right)$ for eight trials.

in the raceway, one order of magnitude above threshold was chosen. Nevertheless, Wisby (1952) reported some avoidance at this concentration. We did not, however, observe any avoidance where the substance was metered into the raceway. It should be noted that concentrations at the delivery tube could be as high as 100 ppm before mixing took place. But, since the substance was delivered immediately below the falls caused by the separating dam, mixing was assumed to be rapid and complete.

Although fish were treated with very low concentrations of the morpholine, EEG responses were not evident until 100 ppm was reached in responsive fish. But, other workers have also found a relative lack of sensitivity with electrophysiological methods. Home-stream responses disappeared with dilution of home-stream water to 5% (Oshima, Hahn, and Gorbman, 1969b), and Sutterlin and Sutterlin (1971), recording from the olfactory epithelium of Atlantic salmon, *Salmo salar*, found no response to morpholine at 0.9 ppm. Yet Wisby (1952) got clear behavioral manifestations of perception at concentrations of 10^{-6} ppm.

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7307

NOTES

OLFACTORY ELECTROENCEPHALOGRAPHIC RESPONSES OF HOMING COHO SALMON, *ONCORHYNCHUS KISUTCH*, TO WATER CONDITIONED BY CONSPECIFICS[1]

Experimental determination of the home stream of migrating salmon is an important technique for elucidating possible orienting cues. Responses are observed in the fish that are specific to the home-stream water and weaken with increasing dilution.

Two techniques have been employed with some success: Idler et al. (1961) and Fagerlund et al. (1963) found that homed salmon made consistent unconditioned behavioral responses to the water to which they homed. Hara, Ueda, and Gorbman (1965) could electrophysiologically demonstrate unconditioned reponses of the olfactory bulb to the home stream. Hara (1970) in his review states that "this electric response is specific in the sense that it cannot be evoked by water from spawning sites of other groups of breeding salmon."

We undertook an investigation of lake-run coho salmon, *Oncorhynchus kisutch*, to determine whether these fish exhibited specific olfactory bulb responses to home water. We tested salmon from two different home streams, examining responses to waters both on and off the migration routes. Furthermore, our field situation allowed us to assess the effects of the returning adult spawners upon the olfactory quality of the home stream.

Materials and Methods

The experimental fish were hatched from eggs obtained from a Michigan fish hatchery and raised in a Wisconsin hatchery for 1.5 yr. In the spring of 1969 approximately 1 mo prior to smolting, they were placed in small impoundments in tributaries of the Ahnapee River and the Kewaunee River (Kewaunee County, Wis.) to which numerous fish have returned in previous years. After initiation of smolting, they were allowed to leave the ponds and make their way downstream to the rivers and thence to Lake Michigan (Figure 1). In the fall of 1970, the mature fish were trapped in weirs on their return up the respective tributaries. The EEG (electroencephalographic) experiments were conducted within 1 km of the trap at the Ahnapee site.

Our experimental procedure was similar to that used by Hara et al. (1965). The fish was paralyzed with gallamine triethiodide (2 mg/kg), and water was perfused continually over the gills. An electrode was placed near the rear margin of the exposed olfactory bulb. The responses, evoked by perfusion of the ipsilateral naris, were amplified (Bio-electric Instruments, model DS2C[2]) and recorded on a two-channel oscillograph (Hewlett Packard, model 7712B) for later analysis. This oscillograph was equipped with an integrating preamplifier for efficient quantification of bulbar activity. Responses reported later are expressed as the sum of the positive areas under the response wave.

Our procedure differed from that of previous workers in two ways:

1. A monopolar stainless steel microelectrode (Transidyne General, model 415100K) was used instead of a bipolar one. The indifferent electrode was clipped to the contralateral operculum.
2. Instead of direct introduction of stimuli to the naris via a wash bottle, a perfusion apparatus allowed one of four samples to be interspersed between a continuous tap water rinse (1 ml/s). Every 75 s, test water (10 ml) was introduced into the interrupted tap water flow. The median response to each stimulus was then

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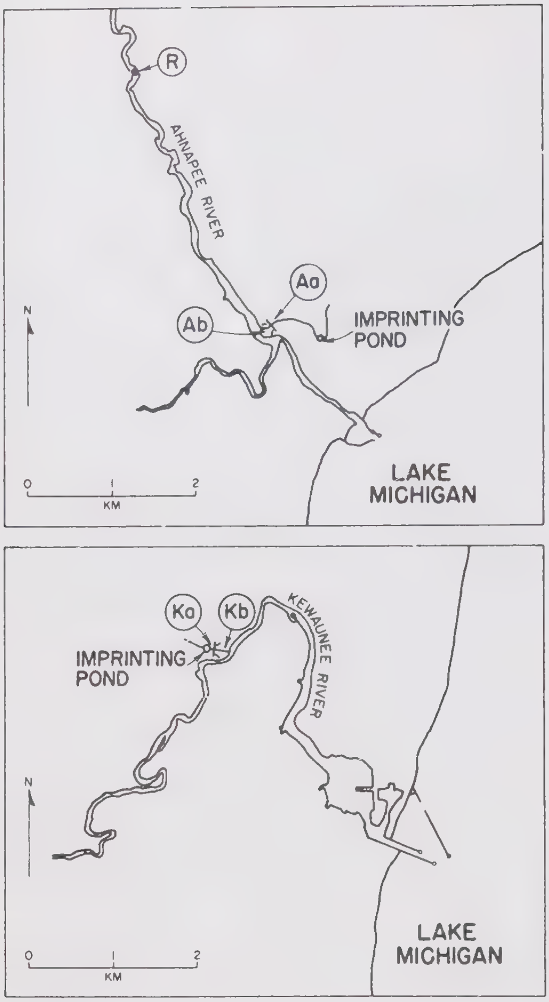

FIGURE 1.—Map of area. Water from Lake Michigan (L) was collected upwind of river mouth.

used in the later analysis. A control series with the same stimulus in each of the four holders demonstrated that delivery through any one of the four sample holders gave comparable results.

Water samples for testing responses of coho salmon were collected from the two home streams (a tributary to the Ahnapee River (A) and a tributary to the Kewaunee River (K)), the Ahnapee River (R) 4 km above the entrance of the home-stream tributary, and Lake Michigan (L) (Figure 1). Samples from the home streams were taken above (Aa, Ka) and below (Ab, Kb) barrier fish traps so that Aa and Ka were home-stream waters while Ab and Kb were home-stream water plus the scents from the returning migrants. Both home streams (A, K) had similar physical features and coho salmon stocking histories; but the tributary to the Kewaunee River (K) contained a greater proportion of well water than stream water compared with the tributary to the Ahnapee River (A).

All sample presentations were made in groups of four to each fish, and responses were quantified as a ratio to the response to water from station Ab. This water sample was included as one of the four presentations for all fish and was chosen as a base because it evoked intense responses. Nineteen Ahnapee fish were tested: 11 with water samples from Aa, Ab, R, and L; 3 with Aa, Ab, R, and water from an unrelated source; 1 with Aa, Ab, and 2 samples from unrelated sources; and 4 with water from Aa, Ab, Ka, and Kb. Six fish from Kewaunee were tested with water from Aa, Ab, Ka, and Kb. (The water samples from other sources showed no consistent patterns and will not be discussed.)

Results

For the Ahnapee fish, samples from the terminus of the return migration evoked greater responses than the sample from the origin (L). But this result is probably not an example of Hara's (1970) "specific electric" response to the home stream: (1) One-half of the "stimulus strength" was added at the trap, although water collected above the trap (Aa) must be considered home stream (Table 1). (2) Agreement on order of responses to each water (Ab>Aa>R>L) was good among fish [$W = 0.87$, $k = 11$, $N = 4$, $P<0.01$ Kendal coefficient of concordance test (Siegel, 1956)], but the absolute difference in responses between presumably nonhome water from the Ahnapee River (R) and home water (Aa) was small. (3) Six fish collected from the Kewaunee River and four controls from the Ahnapee site were tested with water collected at Ab and Aa and from the corresponding stations from Kewaunee, Kb, and Ka. Kewaunee fish responded to their home-stream water more

TABLE 1.—Median EEG response ratios of coho salmon[1] from two different spawning sites to waters collected both on and off their migration route.

Water sample collection point	Number of fish	Quartile Responses		
		1st	2d	3d
Ahnapee fish:				
Aa	19	0.40	0.50	0.67
R	14	.14	.37	.47
L	11	0	.07	.21
Kb	4	.16	.28	.35
Ka	4	.04	.10	.18
Kewaunee fish:				
Aa	6	.36	.46	.55
Kb	6	.19	.25	.55
Ka	6	0	.06	.12

[1] Response ratio $\left[\frac{\text{response to sample}}{\text{response to Ahnapee tributary below (Ab)}}\right]$.

strongly if the water was taken from below the traps (Kb) than from above the traps (Ka). Furthermore, Kewaunee fish responded to Ahnapee home-stream water more than to their own (Table 1). Yet the Kewaunee fish did home correctly — three of the six Kewaunee fish carried fin clips unique to that site (the other three were unmarked).

Discussion

Hara (1970) in his recent review of electrophysiological studies of olfactory discrimination by homing salmon, concluded that "each spawning area has its own specific stimulant, or special combination of stimulants, recognized and responded to by the anadromous salmon." He acknowledged both that EEG responses of returning salmon adults can indicate a recognition of a chemical factor from conspecifics and that recent exposure of mature salmon to nonhome-stream water can result in strong EEG responses to that water (Oshima, Hahn, and Gorbman, 1969). Therefore olfactory responses to the home stream could result from (1) natal imprinting (a long-term memory), (2) recent exposure to the water (a short-term memory), (3) recognition of chemical factors from conspecifics, (a genetic (?) memory), and (4) the presence of stimulatory products not in any way specific to the home stream, transient, and incidental to the salmon's appearance, past or present, in the stream (responses independent of memory).

Our work appears to be the first to separate responses to conditioned home-stream water (other conspecifics were present) from responses to "pure" home-stream water. Conditioning of water by conspecifics appeared to double the EEG response to the home stream.

Perception of factors in the home stream other than those contributed by conspecifics is indicated in the greater responses of the Ahnapee coho salmon to "pure" home-stream water (Aa) than to other waters (R, M) not strongly conditioned by conspecifics. But this result does not necessarily imply natal imprinting (long-term memory) or recent exposure (short-term memory). Perception of nonspecific odoriferous products is indicated since (1) responses to water from the home stream (Aa) and nonhome river (R) by Ahnapee fish differ little, and (2) Kewaunee fish responded more to "pure" water from the Ahnapee tributary than to their own home-stream water.

The consistence of ranking of the four test waters (Ab>Aa>R>L) by 11 fish indicates some degree of reliability of the electrophysiological technique. Nevertheless, there seems to be an inherent lack of precision associated with evoked bulbar recordings. Sutterlin and Sutterlin (1971) found that EEG responses varied greatly among and within fish when compared to simultaneous olfactory epithelium recordings. Furthermore, our collection stations for water samples were subject to seiches (reversed current flow in the river and stream) and variable rates of river and stream discharge that made the water inconstant.

In conclusion, our experiments with lake-run coho salmon indicate the need to clearly differentiate between responses to "pure" home-stream water and water conditioned by presence of conspecifics. An intense and apparently specific response to home-stream water is not necessarily indicative of juvenile olfactory imprinting.

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7308

Subpoint Prediction for Direct Readout Meteorological Satellites

L. E. EBER[1]

ABSTRACT

The National Environmental Satellite Service (NESS) provides orbital information on meteorological satellites with direct transmission systems, through APT (Automatic Picture Transmission) Predict messages sent over standard weather communications networks. With periodic access to this information, operators of independent APT ground receiving stations can extrapolate, by means of nodal period and nodal increment, to determine future orbits within receiving range of their station. A technique for the prediction of subpoint location along an orbit as a function of time after ascending node was developed from consideration of Kepler's laws and derived expressions for the force due to the earth's gravitational potential. Subpoint latitudes and longitudes computed by this technique are within 0.1 degree of those given in NESS predictions.

INTRODUCTION

Users of APT (Automatic Picture Transmission) and Direct Readout Scanning Radiometer data from meteorological satellites, who operate APT ground receiving stations, need orbital information for scheduling transmission pickup and for tracking and locating subpoints for data identification. Such information is provided by the National Environmental Satellite Service (NESS) through APT Predict messages transmitted over meteorological teletype circuits.[2] In cases where these messages are not regularly available, or where advance scheduling is desired, the dates, times, and longitudes of the ascending nodes for selected orbits can be extrapolated by means of nodal period and nodal increment as much as a month ahead with acceptable accuracy. Subpoint locations at selected time invervals along the track also can be predicted for future orbits if certain other orbital characteristics are known. These include the semimajor axis and eccentricity of the orbital ellipse, the orbital inclination, and the geocentric angle of the perigee measured, at a known reference time, from the ascending node in the orbital plane.

UNDISTURBED ORBITAL MOTION

The orbit of a meteorological satellite is an ellipse with the earth's center at one focus. According to Kepler's laws, the motion of a satellite is such that a ray from the focus to the satellite sweeps out equal areas in equal times. Consequently the angular velocity of the satellite is greatest at perigee when the satellite is at its nearest approach to the earth and least at apogee when it is farthest away. The area swept out per unit time by the satellite can be expressed by:

$$\frac{R^2 d\ \alpha}{2dt} = \frac{\pi AB}{P}$$

where $d\ \alpha/dt$ is the angular velocity, R is the distance from the center of the earth to the satellite, A and B are, respectively, the semimajor and semiminor axes of the orbital ellipse, and P is the orbital period. Rearrangement of terms gives an explicit equation for the angular velocity, as follows:

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[1] Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

[2] ESSA (Environmental Science Services Administration) Direct Transmission System Users Guide, prepared by the National Environmental Satellite Center, U.S. Department of Commerce, 1969.

$$\frac{d\alpha}{dt} = \frac{2\pi AB}{PR^2}. \qquad (1)$$

The values of A and B are related to the eccentricity, e, of an ellipse by the expression

$$e = \frac{F}{A}$$

where

$$F = \sqrt{A^2 - B^2}$$

and represents the distance from the center to either focus of the ellipse.

The relation between R and α can be obtained from the basic equation of an ellipse in polar coordinates, with the origin at one focus and the polar axis coincident with the major axis of the ellipse:

$$R = \frac{A\,(1 - e^2)}{1 \pm e \cos \alpha}. \qquad (2)$$

DISTURBED ORBITAL MOTION

Because the earth is not a concentrically homogeneous sphere, but rather an oblate ellipsoid of revolution, the angular velocity is not exactly defined by Equation (1). The elliptic motion is governed by a force which can be defined in terms of the Newtonian gravitational potential U, as follows (Menzel, 1960):

$$U = \frac{K^2 M}{R} + \frac{K^2 (I - J)(1 - 3 \sin^2 \phi)}{2R^3} \qquad (3)$$

where M is the mass of the earth,
- K^2 is the constant of gravitation,
- I is the moment of inertia about the polar axis,
- J is the moment of inertia about any diameter in the earth's equatorial plane, and
- ϕ is the angle between the equatorial plane and a line from the earth's center to the satellite (i.e., ϕ = latitude).

The expression $(I - J)$ can be related to the earth's mass M, the equatorial radius a, the earth's flattening f, and the ratio q of the earth's centripetal acceleration at the equator to gravity, as follows:

$$I - J = (2/3)\, Ma^2\, (f - q/2). \qquad (4)$$

Substituting Equation (4) in Equation (3), we get

$$U = \frac{K^2 M}{R} + \frac{K^2 Ma^2 (f - q/2)(1 - 3 \sin^2 \phi)}{3R^3}. \qquad (5)$$

A more precise form of expression for the earth's gravitational potential is given in terms of spherical harmonics by

$$U = \frac{K^2 M}{R} - \frac{K^2 M}{R} \sum_{n=2}^{\infty} J_n \left(\frac{a}{R}\right)^n P_n (\sin \phi)$$

where the J_n are constants which can be determined from observations of earth satellites, and the $P_n (\sin \phi)$ are Legendre polynomials (Runcorn, 1967). The first term in the series (corresponding to $n = 2$) represents the main effect of the earth's oblateness. The value of J_2 has been determined as 1.0826×10^{-3}, which is 400 times greater than J for any of the higher n. The Legendre polynomial for $n = 2$ is

$$P_2 (\sin \phi) = (3/2) \sin^2 \phi - 1/2.$$

If terms in higher n are omitted, the expression for gravitational potential becomes

$$U = \frac{K^2 M}{R} + \frac{K^2 M\, a^2 J_2\, (1 - 3 \sin^2 \phi)}{2R^3}.$$

This expression is equivalent to Equation (5) if terms of second and higher order are omitted in the following relation between J_2 and the constants f and q:

$$J_2 = (2/3)\,(f - q/2) - (1/3)\, f^2 + (1/2) q^2 + (2/21) fq.$$

The values of f and q have been determined as 3.353×10^{-3} and 3.468×10^{-3}, respectively, so that

$$(2/3)\,(f - q/2) = 1.0794 \times 10^{-3}.$$

The value of K^2M is 3.986×10^5 km^3 sec^{-2}.

The gravitational acceleration is obtained by differentiating (5) with respect to R to get

$$\frac{dU}{dR} = \frac{-K^2 M}{R^2} - \frac{K^2 Ma^2 (f - q/2)(1 - 3\sin^2\phi)}{R^4}. \qquad (6)$$

This expression for gravitational acceleration due to the mass of the earth could be equated directly to the centripetal acceleration of an earth satellite if it were traveling in a true circular orbit. In an elliptical orbit, however, there is a deviation from circular motion which can be identified by substituting into (1) the following expression from Kepler's third law for the orbital period:

$$P = \frac{2\pi A^{3/2}}{K\sqrt{M}}.$$

The substitution gives

$$\frac{d\alpha}{dt} = \frac{KAB}{R^2}\sqrt{\frac{M}{A^3}}, \qquad (7)$$

from which we obtain the following equation for centripetal acceleration:

$$R\left(\frac{d\alpha}{dt}\right)^2 = \frac{K^2 M B^2}{R^3 A}. \qquad (8)$$

The right side of Equation (8) can be considered as the product of (B^2/RA) and the quantity (K^2M/R^2). The latter is equivalent, except in sign, to the first term on the right side of Equation (6) and represents the gravitational acceleration for undisturbed motion. The correction for the ellipticity of an orbit is contained in the factor B^2/RA. Its value approaches 1 when an orbit is nearly circular. By applying this factor to the right side of Equation (6) we can relate the earth's gravitational acceleration to the centripetal acceleration of an earth satellite as follows:

$$R\left(\frac{d\alpha}{dt}\right)^2 = \frac{B^2}{RA}\left(\frac{K^2M}{R^2} + \frac{K^2Ma^2 (f - q/2)(1 - 3\sin^2\phi)}{R^4}\right),$$

and the angular motion is

$$\frac{d\alpha}{dt} = \frac{B}{R}\left(\frac{K^2M}{R^2A} + \frac{K^2M a^2 (f - q/2)(1 - 3\sin^2\phi)}{R^4A}\right)^{1/2}. \qquad (9)$$

SUBPOINT LOCATION

Satellite orbit predictions are given in terms of subpoint locations at fixed intervals of time following the northward equator crossing, referred to as the ascending node. Numerical integration of Equation (9), carried out with suitably small time increments, can be made to yield successive values of α requisite for subpoint computation. If α is taken to be zero when the satellite is at perigee, then the plus sign preceding $e \cos \alpha$ in Equation (2) is applicable and R is given by

$$R = \frac{A(1 - e^2)}{1 + e\cos\alpha}. \qquad (10)$$

R can be computed from Equation (10) for each iteration in the numerical integration of Equation (9) using the value of α from the preceding iteration increased by one-half the average angular displacement $[360\,(\triangle t)/2P]$ during the selected time increment, $\triangle t$. In order to start the numerical integration of Equation (9) at the ascending node, an initial value of α must be determined from the orientation of the orbital ellipse. The latter is expressed as the argument of perigee, which is the geocentric angle of the perigee measured in the orbital plane from the ascending node in the direction of motion. The

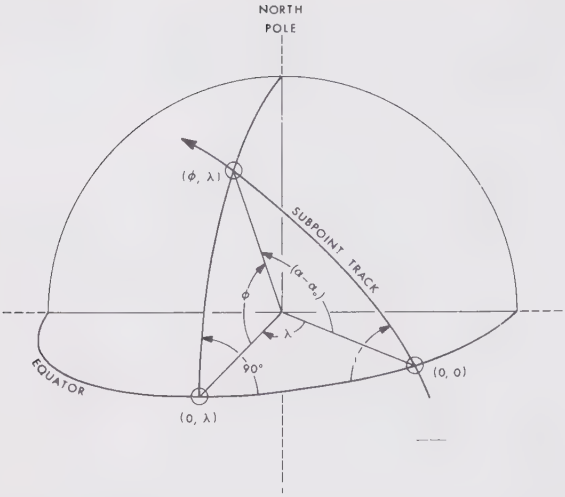

Figure 1.—Right spherical triangle formed by the equator, the orbital subpoint track and the meridian through the subpoint (ϕ, λ).

initial value of α is obtained by subtracting the argument of perigee from 360°.

The gravity effect of the earth's equatorial bulge causes the perigee to shift slightly during each orbit. Consequently, it is necessary to know the rate at which the orbital ellipse is shifting in order to determine the correct initial values of α for prediction of future orbits.

The locus of orbital subpoints for an earth satellite traces a great circle on a sphere concentric with the earth. Each subpoint can be represented by a pair of coordinates (ϕ, λ), where ϕ is the geocentric latitude and λ is the longitudinal displacement of the subpoint measured from the longitude of the ascending node. Subpoint coordinates corresponding to any point of the orbit can be determined from its angular displacement, measured along the orbital track from the ascending node. If α is the angular coordinate (measured from perigee, as defined in the preceding section) and α_0 is the value of α at the ascending node, the angular displacement is $(\alpha - \alpha_0)$. Figure 1 shows these quantities as components of a right spherical triangle whose vertices are defined by the subpoint (ϕ, λ), the coordinates of the ascending node $(0, 0)$ and the point $(0, \lambda)$. The two sides forming the right angle are ϕ and λ respectively. The opposite side is $(\alpha - \alpha_0)$ and is a segment of the subpoint track. The angle opposite ϕ, denoted by i, is the inclination of the orbital plane to the equatorial plane. Application of the trigonometric formulas derived from Napier's rules yields the following relationships:

$$\sin \phi = \sin(i)\sin(\alpha - \alpha_0), \qquad (11)$$

$$\tan \lambda = \cos(i)\tan(\alpha - \alpha_0), \text{ and} \qquad (12)$$

$$\tan \phi = \tan(i)\sin \lambda. \qquad (13)$$

Equations (11) and (12) give explicit formulas for ϕ and λ as a function of (i) and $(\alpha - \alpha_0)$. Equation (13) represents the great circle traced by the orbital subpoints.

ORBIT PREDICTION

The concepts developed in the preceding sections deal with the computation of satellite subpoints relative to the time and longitude of the ascending node. Application of these concepts to advance preparation of orbit schedules requires, therefore, prediction of the times and longitudes of ascending nodes for future orbits. The APT Predict messages give orbital period to the nearest second and longitudinal displacement per orbit to the nearest hundredth of a degree. This precision is adequate to extrapolate a few orbits ahead. Greater precision is needed for satisfactory extrapolation beyond a hundred orbits and can be obtained from NESS or can be gained by empirical adjustments.

The orbital elements necessary for computation of subpoint locations for extrapolated orbits, also obtainable from NESS, include the length of the semimajor axis, eccentricity, orbital inclination, argument of perigee at a known time or reference orbit, and the rate of change of perigee. The latter is equal to the rate of change of α_0, the value of the angular displacement α at the ascending node, which can be computed from the following expression (Runcorn, 1967):

$$d\,\alpha_0/dt = 4.98(a/A)^{3.5}\ (1 - e^2)^{-2}\,(5 \cos^2 i - 1)$$
(degrees per day),

where e is the eccentricity of the orbital ellipse,
i is the inclination of the orbital plane to the earth's equatorial plane,
a is the earth's equatorial radius, and
A is the semimajor axis of the ellipse, as previously defined.

For the satellite ESSA-8, the value of i is 78.3°, $A = 7815.37$ km, and $e = 0.00323$. With these values and taking 6378 km for a, we compute

$$\frac{d\,\alpha_0}{dt} = -1.943 \text{ deg per day.}$$

Given the nodal period of ESSA-8 as 115.703 min we find, alternately, that

$$\frac{d\,\alpha_0}{dt} = -0.15476 \text{ deg per orbit.}$$

The minus sign indicates that the change is opposite to the angular motion of the satellite.

Having determined α_0 for a selected orbit and starting at the ascending node where $\alpha = \alpha_0$, the radial distance R can be computed from Equation (10) for use in the numerical integration of Equation (9), to yield the angular displacement $(\alpha - \alpha_0)$ for successive intervals of desired length after the time of ascending node. The values of ϕ and λ can then be obtained with Equations (11) and (12). These are the spherical coordinates of the point of the orbit relative to a nonrotating frame of reference with origin at the earth's center.

In order to plot the subpoint track on a chart, the spherical coordinates of points on the orbit need to be transformed to the geographic (geodetic) latitudes and longitudes of the corresponding subpoints. The latter are the locations on the earth's surface where the local vertical passes through the satellite. The angle which local vertical makes with the equatorial plane defines the geodetic latitude of the subpoint (Bowditch, 1958). Owing to the earth's ellipsoidal shape, a line from the satellite to the center of the earth intersects the surface at a point north of the satellite subpoint. The geodetic latitude at this point of intersection is a close approximation to that of the subpoint and can be computed from the following expression:

$$\text{geodetic latitude} = \text{arc ctn}\,[(1 - q)\text{ ctn }\phi]$$

where q is the ratio of centripetal acceleration at the equator to gravity, as defined earlier. This expression is derived from the vector difference between the true force of gravitation on a unit mass at a point on the earth and the apparent force of gravity at that point, as a result of the earth's rotation. Taking

$$q = 3.468 \times 10^{-3}$$

the maximum correction for geodetic latitude computed with the above expression is about 0.1 degree at latitude 45 degrees.

The longitude of the satellite subpoint can be obtained by adding the longitude of the ascending node to the value of λ computed with Equation (12). Adjustment for the earth's rotation is made by adding to this sum the product of the rate of rotation (0.25 degree of longitude per minute) and the elapsed time from the ascending node to the point of the orbit for which the subpoint location is desired. A correction must be made for the precession of the orbital plane which, in a sun-synchronous orbit, amounts to 360 degrees in 365 days and is subtractive.

APPLICATION

The foregoing procedures have been implemented in a computer program for preparing orbit schedules at the Southwest Fisheries Center, La Jolla Laboratory, National Marine Fisheries Service. The program includes a section for each active satellite in which appropriate values are assigned for semimajor axis, eccentricity, inclination, anomalistic period, argument of perigee at a known reference orbit and the rate of change of the argument of perigee. All of these quantities are taken directly from information sheets furnished by NESS.

In running the program, a data card is submitted for each schedule to be printed. On it are punched the name of the satellite and the orbit number, day, hour, minute, second, and longitude of the ascending node for a particular orbit as read from a recent or current APT Predict message. The card is also punched with the standard (or daylight) time zone at the station for conversion from universal to local time, and a specification of the number of minutes after ascending node to which computed orbit reference times will apply. The latter tells the APT ground station operator when to expect to begin receiving transmission. The number specified indicates to the program whether orbits selected for subpoint computation are to be determined by south-to-north or north-to-south traverses over the station.

```
ORBIT SCHEDULE FOR  ESSA-8  OCT 21-28

   INITIAL DATA:  17637  20  13  31  32  22628      8

   ORBIT REFERENCE TIMES ARE 36 MINUTES AAN (PST)

                                SUBPOINT LOCATIONS AT ONE MINUTE INTERVALS
                            MIN  LAT     LON    MIN  LAT     LON    MIN  LAT     LON    MIN  LAT     LON    MIN  LAT     LON
DATE: 21  ORBIT17651         37  60.95   82.59   38  58.06   85.32   39  55.13   87.67   40  52.17   89.74   41  49.18   91.58
HR  8  MIN 53  SEC 23        42  46.18   93.23   43  43.15   94.74   44  40.12   96.13   45  37.08   97.43   46  34.02   98.64
LONG ASC NODE:  84.82E       47  30.96   99.78   48  27.90  100.87   49  24.83  101.92   50  21.75  102.92   51  18.68  103.99
                             52  15.60  104.84   53  12.52  105.77   54   9.43  106.68   55   6.35  107.58   56   3.27  108.47

DATE: 21  ORBIT17652         37  60.95  111.27   38  58.06  113.99   39  55.13  116.35   40  52.17  118.41   41  49.18  120.25
HR 10  MIN 48  SEC  5        42  46.18  121.91   43  43.15  123.42   44  40.12  124.81   45  37.08  126.10   46  34.02  127.31
LONG ASC NODE:  56.14E       47  30.96  128.46   48  27.90  129.55   49  24.83  130.59   50  21.75  131.60   51  18.68  132.57
                             52  15.60  133.52   53  12.52  134.44   54   9.43  135.35   55   6.35  136.25   56   3.27  137.14

DATE: 22  ORBIT17664         37  60.94   95.38   38  58.06   98.11   39  55.13  100.46   40  52.17  102.52   41  49.18  104.36
HR  9  MIN 44  SEC 31        42  46.17  106.02   43  43.15  107.53   44  40.12  108.92   45  37.08  110.21   46  34.02  111.42
LONG ASC NODE:  72.03E       47  30.97  112.57   48  27.90  113.66   49  24.83  114.70   50  21.76  115.71   51  18.68  116.68
                             52  15.60  117.63   53  12.52  118.55   54   9.44  119.46   55   6.36  120.36   56   3.28  121.25

DATE: 23  ORBIT17676         37  60.94   79.49   38  58.05   82.22   39  55.12   84.57   40  52.16   86.63   41  49.18   88.47
HR  8  MIN 40  SEC 57        42  46.17   90.13   43  43.15   91.64   44  40.12   93.03   45  37.08   94.32   46  34.03   95.53
LONG ASC NODE:  87.92E       47  30.97   96.68   48  27.90   97.77   49  24.83   98.81   50  21.76   99.81   51  18.69  100.79
                             52  15.61  101.73   53  12.53  102.66   54   9.45  103.57   55   6.37  104.47   56   3.28  105.36

DATE: 23  ORBIT17677         37  60.94  108.17   38  58.05  110.89   39  55.12  113.25   40  52.16  115.31   41  49.18  117.15
HR 10  MIN 35  SEC 39        42  46.17  118.80   43  43.15  120.31   44  40.12  121.70   45  37.08  123.00   46  34.03  124.21
LONG ASC NODE:  59.25E       47  30.97  125.35   48  27.90  126.44   49  24.83  127.49   50  21.76  128.49   51  18.69  129.46
                             52  15.61  130.41   53  12.53  131.34   54   9.45  132.25   55   6.37  133.14   56   3.29  134.03

DATE: 24  ORBIT17689         37  60.94   92.28   38  58.05   95.00   39  55.12   97.36   40  52.16   99.42   41  49.18  101.26
HR  9  MIN 32  SEC  6        42  46.17  102.91   43  43.15  104.42   44  40.12  105.81   45  37.08  107.10   46  34.03  108.32
LONG ASC NODE:  75.14E       47  30.97  109.46   48  27.91  110.55   49  24.84  111.59   50  21.77  112.60   51  18.69  113.57
                             52  15.61  114.52   53  12.54  115.44   54   9.46  116.35   55   6.37  117.25   56   3.29  118.14

DATE: 24  ORBIT17690         37  60.94  120.96   38  58.05  123.68   39  55.12  126.03   40  52.16  128.10   41  49.18  129.93
HR 11  MIN 26  SEC 48        42  46.17  131.59   43  43.15  133.10   44  40.12  134.49   45  37.08  135.78   46  34.03  136.99
LONG ASC NODE:  46.46E       47  30.97  138.14   48  27.91  139.23   49  24.84  140.27   50  21.77  141.27   51  18.69  142.25
                             52  15.61  143.19   53  12.54  144.12   54   9.46  145.03   55   6.38  145.93   56   3.29  146.92

DATE: 25  ORBIT17702         37  60.94  105.07   38  58.05  107.79   39  55.12  110.14   40  52.16  112.21   41  49.18  114.04
HR 10  MIN 23  SEC 14        42  46.17  115.70   43  43.15  117.21   44  40.12  118.60   45  37.08  119.89   46  34.03  121.10
LONG ASC NODE:  62.35E       47  30.97  122.25   48  27.91  123.33   49  24.84  124.38   50  21.77  125.38   51  18.70  126.35
                             52  15.62  127.30   53  12.54  128.23   54   9.46  129.14   55   6.38  130.03   56   3.30  130.92
```

Figure 2.—Example of computer generated satellite orbit schedule with subpoint locations for selected orbits.

TABLE 1.--Verification of computed subpoint locations for ESSA-8. Computed values minus APT Predict values are given in degrees latitude or longitude.

Min AAN*	Approximate latitude	Orbit 15239 (4/12/72)		Orbit 15641 (5/14/72)		Orbit 16030 (6/14/72)		Orbit 16444 (7/17/72)		Orbit 16846 (8/18/72)		Orbit 17235 (9/18/72)		Orbit 17637 (10/20/72)	
		Lat	Long	Lat	Long	Lat	Long	Lat	Long	Lat	Long	Lat	Long	Lat	Long
34	70°	.05	.00	.04	-.01	.06	.00	-.01	-.02	.04	-.02	.00	.06	.00	-.03
36	64°	.03	-.03	.06	.02	.05	-.01	.01	-.01	.03	.00	-.02	-.02	.09	.00
38	59°	.00	.03	.06	-.04	.01	-.01	-.01	.07	-.03	-.02	.00	-.01	.06	-.05
40	53°	.01	.06	.01	-.01	-.01	.01	-.02	.00	.01	.00	.01	.01	.07	-.03
42	47°	.01	.07	.05	-.02	-.04	.07	.05	.03	.04	.02	.00	.06	.08	-.03
44	41°	.05	-.03	.03	-.01	-.03	.01	.04	.02	-.01	.01	.03	.00	.02	-.03
46	35°	.04	-.02	.06	-.01	.03	.05	-.01	-.01	.00	-.02	.01	.04	.02	-.02
48	29°	.01	.02	.07	.03	.06	.00	-.01	.07	.06	.06	.05	.00	.10	.01
50	22°	.05	-.03	.06	-.02	.06	.07	.07	.05	-.01	.04	.08	.06	.05	.06
52	16°	.09	-.01	.03	.00	.05	.00	.02	-.01	.01	-.02	.09	.00	.09	.02
54	10°	.12	.03	.10	.03	.02	.04	.06	.04	.01	.04	.09	.04	.03	.02
56	4°	.04	.02	.06	.01	.08	.02	.08	.04	.00	.04	.09	.04	.06	.01

*Minutes after ascending node.

A sample schedule, computed and printed for ESSA-8, is shown in Figure 2. ESSA-8 transmits only during the daytime, when it is following a north-to-south track. Accordingly, the reference time appearing to the left of each set of subpoint tabulations is 36 min later than the time of ascending node for the orbit indicated. The numbers labeled "INITIAL DATA" were read from the data card and are printed for verification. The subpoint locations are printed to the nearest hundredth of a degree of latitude or longitude, for each minute from 37 to 56 min after ascending node, which covers the daytime track from about lat. 60° N to lat. 4° N. The subpoint location corresponding to a picture transmitted by the satellite can be found by interpolation, based on determination of the time of the picture relative to the time of ascending node. The schedule includes only those orbits within range of the APT ground station at the La Jolla Laboratory.

A comparison of computed subpoint locations with those given in APT Predict messages for seven orbits of ESSA-8, completed between April and October 1972, is presented in Table 1. Subpoint locations are given to the nearest tenth of a degree in APT Predict messages, while computed values were carried to the nearest hundredth of a degree. Differences between computed values and corresponding APT Predict values averaged less than 0.06 degree of latitude or longitude. Since ESSA-8 completes an orbit in a little less than 2 hr, the motion of the satellite subpoint is about 3 nautical miles per second. An error of 0.05 degree latitude (equal to 3 nautical miles) in subpoint location is equivalent, therefore, to an error of about 1 sec in determining the time of an observation from the satellite.

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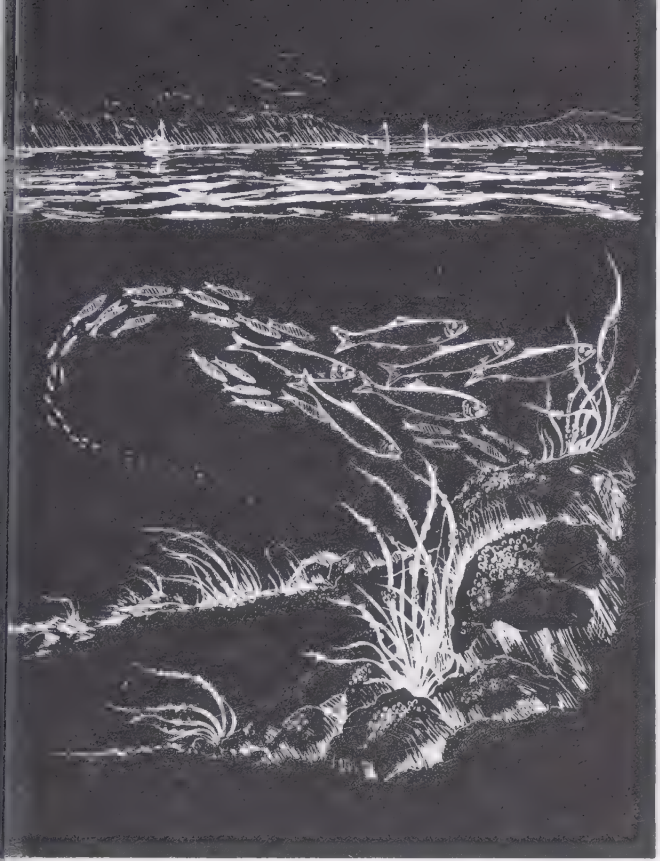
MFR PAPER 1018



In a classic conflict, herring tests the ability of the political process to manage a renewable natural resource.

San Francisco Bay Area's Herring Resource — A Colorful Past and a Controversial Future

MAXWELL B. ELDRIDGE
and W. MICHAEL KAILL

INTRODUCTION

Discuss Pacific herring with the people of Tomales Bay or the northern counties of San Francisco Bay (Figure 1) and you will very likely encounter the two edges of a sharp sword. The sword aims at a fish resource which has become a classic example of the conflict over natural resources. The issue is still unsettled.[1] The Pacific herring fishery remained quiescent over the last two decades, and there has been little interest shown for management of the population. The fishery landed 53,235 pounds five years ago and only 21,700 pounds during the 1971-72 season. Then a new market opened this last winter and the catch rose to over 2 million pounds. The rush to the harvest brought attention from local conservationists and legislators. Their efforts resulted in legislation which effectively controlled the herring fishery.

This paper includes some historic background of the San Francisco Bay area Pacific herring (*Clupea harengus pallasi*) which predates the gold rush days. It discusses the known biology of the herring and the research being conducted to find out more about the species. Lastly, it presents the latest in a series of events which may ultimately determine the fate of this population of fish.

HISTORY OF THE RESOURCE

Studies of the bottom sediment of Tomales Bay showed that Pacific herring were residents of the San Francisco Bay area waters long before it was colonized by man. San Francisco was just a sleepy town with only 375 inhabitants as recently as 1847. In those early times, the local fish resources, including herring, remained relatively untouched. Then gold was discovered, and within two years the population rose to 25,000 people. With this growth came a demand for food. The first interest in herring was for fresh fish which were sold for "two bits a bucketful." The only export interest at that time was in rough salted fish which were sent to the Orient.

The fishery grew slowly; small amounts were used for smoking, curing, and canning. Attempts to export local herring to Europe to compete with Atlantic herring met with limited success. With continued efforts and the advent of World War I there eventually arose a large demand for Pacific herring for canning and reduction to oil and meal. The catch rose to 8 million pounds by 1918 (Figure

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[1] Data and events current as of 23 August 1973

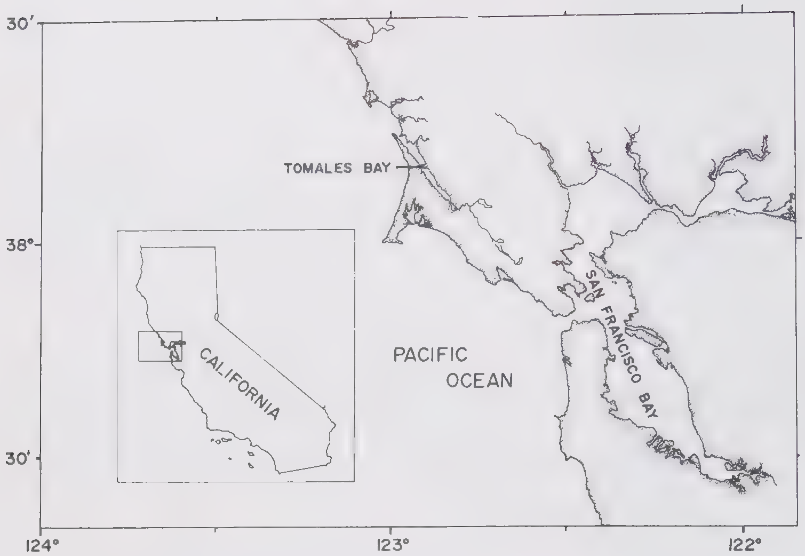

Figure 1.—Map of the San Francisco Bay area.

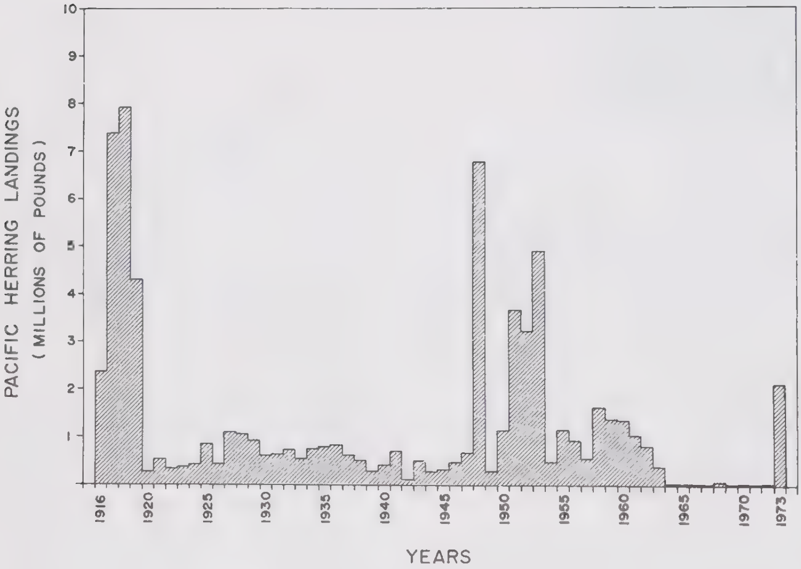

Figure 2.—Pacific herring landings of the San Francisco Bay area (Tomales and San Francisco Bays).

2). At that time the Tomales Bay herring were considered the best in California—they were fatter and longer. The fish were brought from Tomales Bay on a narrow gauge railroad to the city of Sausalito, in San Francisco Bay, then shipped upriver to canners in the Sacramento River delta. The Federal Bureau of Fisheries advised the fishery in its curing and processing. The herring were Scotch cured and canned. It was the first time the fishery was tested for its capacity and it was believed that the herring take could be doubled and still not damage the resource.

In 1919 the California State Reduction Act was passed which prohibited reduction without written permission from the California Department of Fish and Game. This legislation effectively reduced landings of herring to an all time low. The fishery returned to landing small quantities for fresh consumption (bait, smoked, and salted). This trend continued from 1920 to 1946.

With the decline of the California sardine fishery, herring became a hopeful substitute for the sardine. Canning operations began again with herring trucked in from Tomales Bay. In the early and mid-fifties boats with lampara nets sailed from Monterey to Tomales Bay, where catches brought large increases in the recorded landings (Figure 2). The Bay Area catch rose to 3.6 million pounds. However, herring proved unsuitable as a sardine substitute, and only a small pet food market continued to provide a limited demand. But even this market did not hold and the catch declined to a little over 30,000 pounds by 1964. The main use until recently has been bait.

A new fishery began in 1965-66 related to the herring eggs themselves. The products are exported to Japan as gourmet food. The roe is utilized in two forms. "Kazunoko" is entirely roe, usually the whole ovary. "Kazunoko-kombu" is the herring eggs-on-kelp product. Both are expensive specialty foods, usually consumed on holidays and special occasions.

A permit was issued for 5 tons of herring eggs-on-kelp in Tomales Bay and 5 tons in San Francisco Bay. The permit for Tomales Bay was later cancelled for two seasons to allow the Department of Fish and Game to study the resource. This permit was then reissued this last 1972-73 season. The eggs-on-kelp fishery is still in operation and has been moderately successful. On the basis of Fish and Game Department records, the San Francisco Bay fishery has never collected more than one-half of the quota, and the Tomales Bay fishery approached its quota only once.

The demand for roe was responsible

for a dramatic change in the adult herring fishery this past season. Over 2.1 million pounds of whole adult fish were landed. Due to continued restriction by the 1919 Reduction Act the whole fish could not be reduced in the United States and there was no market for other herring products. Therefore, the fish were frozen in the United States and shipped to Korea for processing. There the roe was removed and sent to Japan while the fish were dried and sold for human consumption in Korea.

The recent tremendous increase in the fishing effort, with its high catches, was one of the reasons for the controversy over the resource.

BIOLOGY OF THE PACIFIC HERRING

Probably, the biggest factor keeping the herring controversy alive and vigorous is the high visibility of the actual fishing operations. The harvesting of both the herring eggs-on-kelp and adult fish takes place in waters adjacent to populated areas. The biological nature of herring is responsible for this.

Unlike the Atlantic herring, which spawns in deeper water, the Pacific herring spawns in the intertidal waters, and in the San Francisco Bay area, they most often spawn along heavily developed shorelines. Although spawning occurs from November to June, peaks of spawning activity occur earlier in the southern populations.

We have netted larvae of the herring in San Francisco Bay as early as late October and early November, long before evidences of the adults are found. Evidently, there is some very limited early spawning. Maturing adults usually enter San Francisco and Tomales Bays up to 2 months before spawning, where they remain in loosely aggregated schools in deep holes.

Observations of the Tomales Bay herring showed that a few days prior to spawning the fish's behavior changes. The schools are more predictably found in the deeper holes of the Bay; the fish exhibit less response to adverse stimuli such as outboard motors, etc., and the densities of the individual schools change. When the right set of conditions prevail, the fish move into intertidal shallows and spawn on any suitable substrate. The fish appear to have preferences for their substrate—choosing first algae and grass, then prominent rocks, and lastly flat surfaces. But once dense spawnings begin, such as occurred in 1971-72, every available surface (including ropes, sandy beaches, and boat hulls) is covered with eggs. The eggs are extremely sticky for a short period after the eggs leave the female. Often it is difficult to remove freshly spawned eggs from one's hands or vegetation without destroying the eggs. Although most spawning seems to occur at night, we have observed spawning taking

place day and night during all tidal stages.

The act of spawning involves repeated passes close to the substrate by females, while males release their milt in the general area. The water often appears "milky" over the entire spawning area.

The eggs are usually deposited 1 or 2 eggs thick but can be in layers up to 2 inches. When the latter occurs we have found very poor survival among all but the outlying eggs.

The most noticeable eggs are those in the intertidal zones—the ones exposed at low tide stages. Actually, the spawning continues subtidally to approximately 25 feet in Tomales Bay and at least that and probably deeper in San Francisco Bay. The fish are usually 3 to 5 years old when they spawn. Work by the junior author showed that over 13 percent of the 1971-72 catch from Tomales Bay was 5 to 8 years old. This is a change from a 1955 study in which less than 3 percent were 5 years old and these were the oldest in the catch. The older age composition of this last year's catch suggests that the population has been under low fishing pressure.

The number of eggs each female produces depends on the size of the fish. For example, a female 7.6 inches long produced 18,600 eggs and one 8.7 inches long had 29,500 eggs.

The incubation time depends mostly on the temperature. Our measurements of the last season's eggs showed the larvae hatched in 10.5 days at an average water temperature of 50.7° F.

Once hatched the larvae are believed to leave the bays. Preliminary results corroborate this belief, although Alaskan and Canadian studies suggest that the juveniles leave the bays in the fall. We have caught large numbers of newly hatched larvae but few of the later stages. Undoubtedly high mortality is a factor on both eggs and larvae as many predators gather at the spawning grounds—gulls and other waterfowl, sturgeon, striped bass, sharks, etc. Depth of water is critical for egg survival. Mortality may range from <5 percent in deep water to 99 percent or more for intertidal spawnings, where the eggs are available to a larger variety of predators.

Where the fish go after they leave the bays is unknown. There is a summer fishery for the adults in Monterey Bay to the south of San Francisco Bay but their origin is also unknown. This past year the state Department of Fish and Game showed that herring could be tagged and survive. If results from Canadian tagging studies are valid for these fish, the local tagging program should show that they move offshore and return to spawn again, using a homing instinct.

Pacific herring make up a series of different intergrading populations from Japan and Korea, north to the Bering Sea and southward along the Pacific coast to Baja California. The population found in the San Francisco Bay area is small compared to those found along the British Columbia coast, where the spawnings are measured in miles of beaches covered with eggs. The San Francisco population is constituted of younger and smaller fish and by slower growth and sexual maturation at younger ages and earlier spawning. The San Francisco population size has been estimated only once, in 1955, at 12,000 tons. The Tomales Bay population was estimated in 1971-72 at approximately 4,000 tons by State biologists and again this last season by the junior author at around 4,000 tons.

Because of the biology of the herring, prediction of forthcoming population size is difficult. Many more eggs are produced than are needed to maintain the population. Losses are high due to predation, exposure, and smothering. Even after the eggs hatch, mortality of larvae, due to predation and drift away from proper food supply, is commonly 99 percent. Those that make it through such a risky early life are still reduced by about half each year. That is, in the process of growing one year older (e.g. three to four years of age) 40 to 60 percent of the population is lost. Because of the interaction of high reproductive potential and high losses due to natural mortality, strange things can happen. Unsatisfactory conditions can cause high mortality of a spawn, regardless of the tonnage of eggs produced. Thus, a poor spawn may produce a very good crop of young fish; or an abundant spawn may produce a poor result, if conditions are poor. Understandably, prediction of the amount of fish produced based on spawning success is difficult. Herring do not enter the shallow water spawning runs until they are two or three years old. Thus, studies based on spawning populations of herring are forced to exclude many of the fish in the total population.

When a spawning does encounter advantageous conditions, many of the fish of that particular spawning (for instance, 1971-1972) survive, producing what biologists call a successful year-class. By studying the age composition of the spawning adult populations it is possible to follow a successful (i.e. abundant) year-class over a number of years.

RESEARCH

Despite the long history of the fishery and the resource, very little biological research was done on the San Francisco Bay area population until recently. In 1955, two State biologists, D. J. Miller and J. Schmidtke, presented results of the commercial catch sampling from 1947 to 1952. They also studied the spawning population that occurred in the winter of 1954-55. In this study, age composition of the population and the density of spawned eggs were determined. The biologists attempted to delimit the school size by echo-sounding equipment when the fish were held up in the deeper portions of San Francisco Bay, but they found the schools too mobile. For the first time, they estimated the

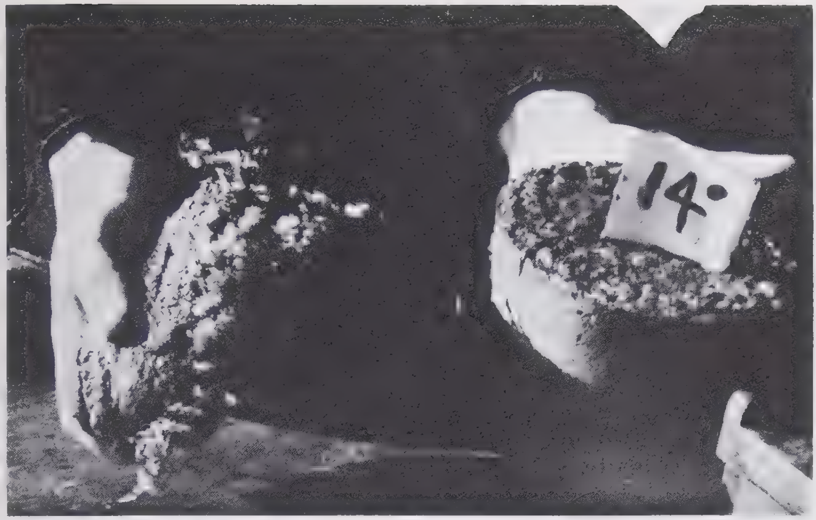

Figure 3.—Examples of a natural rock (left) and artificial spawning substrate used in recent studies of the San Francisco Bay, January 1973.

size of the Tomales and San Francisco populations using the amount of spawned eggs as the measure.

No further work was carried on for another 15 years. Then the herring eggs-on-kelp fishery brought the need for an assessment of the herring egg resource. J. Hardwick, also of the Department of Fish and Game, studied intensively the spawning populations of herring for two consecutive seasons beginning in 1970-71. He surveyed the spawned eggs and vegetation in Tomales Bay using techniques developed by Miller and Schmidtke, and himself. This study was set up to evaluate both the adult fish population and herring eggs-on-seaweed resources. As a result, he recommended that "a harvest of 10 percent (16 tons) of the eggs that hatch would not significantly reduce the number of eggs that hatch," and "should tonnage of whole fish exceed 500 tons it may be necessary to reduce the quota on eggs."

Both the senior and junior authors have conducted independent studies this last 1972-73 spawning season. The senior author's work consisted of two transects or lines of numbered cement discs (Figure 3) which were used for artificial spawning substrates. The commercial catch was sampled to look at the ages, sex ratio, fecundity, and size of the spawners. Preliminary results show a very light spawning in San Francisco Bay this year. The fish hatched in an average 10 days at approximately 50° F water temperature. The fish spawned along the entire transect but lower depths showed lesser egg densities, probably because of poor substrate and high sediment at the deeper locations.

The junior author simultaneously studied the herring in Tomales Bay. The commercial catch was also sampled and an attempt was made to estimate the size of the spawning population by sonar equipment and by surveying the amount of eggs actually spawned in the Bay. Besides the results we have already mentioned other interesting facts were noted.

From observing schools of herring as they became ready to spawn, characteristic behavior was seen which might be of value in predicting the time of spawning. By virtue of the school's compactness and stable positioning, relatively good success was achieved in estimating the volume of herring schools. This could provide a much simpler and less time-consuming method of estimating the population than surveying the actual spawned eggs with the aid of SCUBA gear or by using specialized bottom samplers.

Some answers to questions concerning migration of juvenile and adult fish between spawnings could result from a tag and recovery program begun last year by the State. San Francisco Bay fish were tagged and released after spawning. This next fishing season should show results if the fish, in fact, do remain in or return to local waters.

FISHERY

The methods employed by the commercial fishery over the years are fairly traditional, reflecting the efficacy of those processes. The original fishery used beach seines and gill nets (Figure 4). In 1917, the Bureau of Fisheries advised the fishermen to develop purse seines, lampara nets and larger boats.

The decline of the fishery evidently discouraged such development and the fishing gear and methods did not change until 1952 when lampara boats equipped with sonar equipment fished the populations in Tomales Bay. Up to this last year the same methods have been used, with the introduction of lighters being the only advancement in technology (Figure 5).

The herring eggs-on-kelp are harvested by hand by divers. Since the weather during the spawning season is usually the most inclement time of the year, it is understandable why the quotas have not been filled.

Adult herring have been sold fresh, salted and cured, and attempts at canning have met with varied success. Competition from Atlantic herring and larger northern Pacific herring from Canada and Alaska have made the product not economically profitable. The recent export market includes the sale of dried whole fish to Korea for domestic consumption and the sale of roe to Japan.

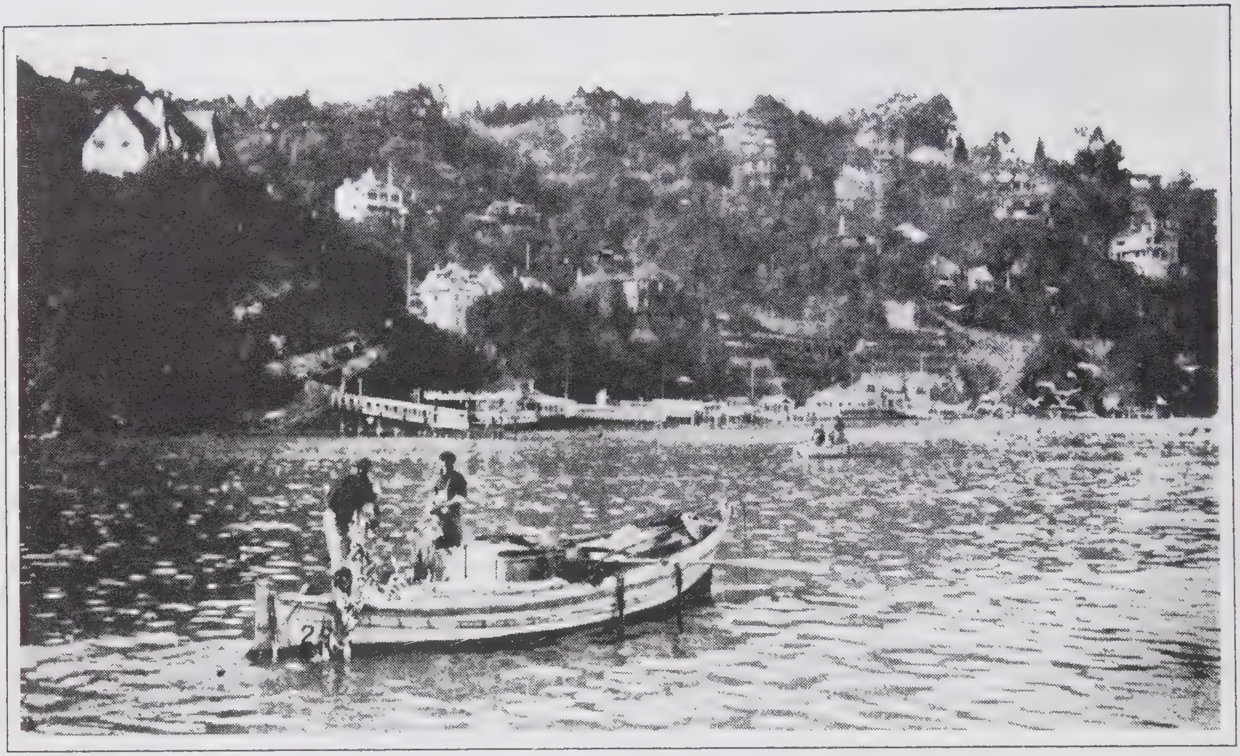

Figure 4.—Herring gill netters at Belvedere Cove, San Francisco Bay, January 1918.

THE DEVELOPING CONTROVERSY

Over 20 years ago the local citizenry openly criticized the fishermen for their use of large boats and new gear which resulted in the large landings of Tomales Bay herring. Now in 1973, essentially the same gear and boats fished the same resource resulting in much the same reaction from the public. The difference, however, is that the most recent public concern was converted to political action limiting the take of herring.

One common feature of both whole fish and eggs-on-kelp fisheries is the high visibility of the fishing activities. Local citizenry, especially some sportsman's organizations were alarmed with what they saw; alarmed to the extent that they persuaded a State Senator to introduce legislation immediately, which subsequently passed, instituting a revocable, nontransferable permit system for harvesting herring and herring eggs in Tomales and San Francisco Bays. It also directed the Department of Fish and Game to develop a management plan and present it to the Commission with the Department responsible for management in the interim period. The bill was signed January 23, 1973, and was operative for 60 days. The Department established quotas of 750 tons for Tomales Bay and 1,500 tons for San Francisco Bay herring. Subsequently, the season in Tomales Bay was closed.

Senator Peter H. Behr, the man who introduced the previous emergency legislation, entered a bill (S.B. No. 502) which prohibits the taking of herring for commercial purposes, except for bait. Another bill (A.B. No. 2309) introduced by Assemblyman Bob Wood at the request of the California Department of Fish and Game, is designed to allow management of the resource through permit issuance by that Department. Both bills are being reviewed by legislative committees.

Whatever decision is made on these bills will most likely be a compromise which will establish a set quota on the fisheries. Thus, a long and heated controversy may soon be resolved as a compromise is reached by legislators acting on information from state, federal, and private research efforts.

The character of the compromise will reflect the ability of a political process to manage a wildlife resource.

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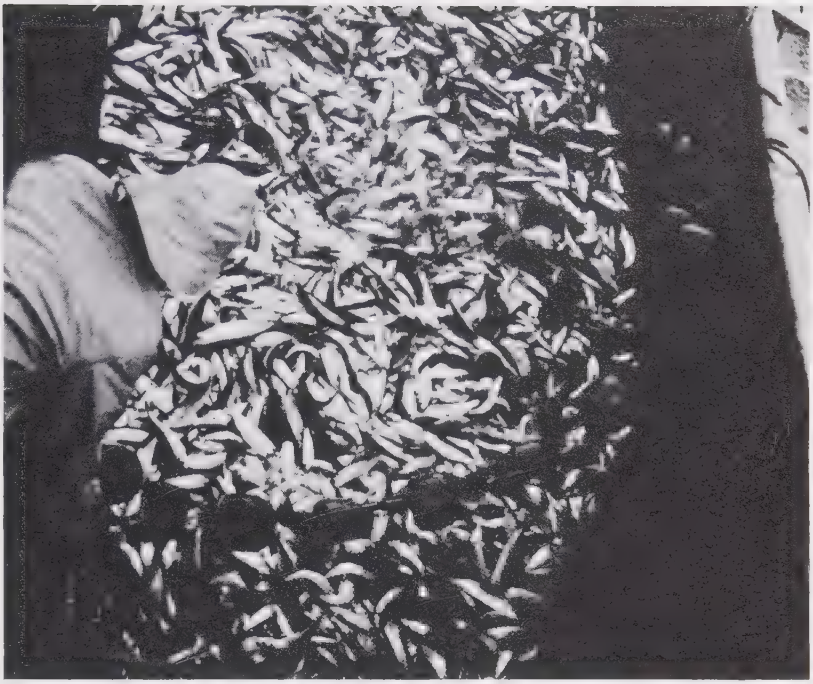

Figure 5.—Lampara net catch of Pacific herring from Tomales Bay, January 1973.

MFR Paper 1018, from Marine Fisheries Review, *Vol. 35, No. 11, November, 1973. Copies of this paper, in limited numbers, are available from D83, Technical Information Division, Environmental Science Information Center, NOAA, Washington, D.C. 20235.*

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A GENERAL LIFE HISTORY EXPLOITED POPULATION SIMULATOR WITH PANDALID SHRIMP AS AN EXAMPLE[1]

WILLIAM W. FOX, JR.[2]

ABSTRACT

A general life history population simulator, GXPOPS, with provisions to exploit any age sector of the population is presented. In addition to the usual fish life history pattern, the model allows simulation of random mating, sex-differential maturation, and stepwise growth found in many crustacean and some fish populations. GXPOPS provides for monthly calculations and all rates may be as general as month specific. The generality of the model is illustrated with an examination of closed season management strategies for a pandalid shrimp population.

The advent of the digital computer has allowed simulation modeling to become the current vogue within nearly all fields of science; fisheries is no exception. The computer has freed mathematically inclined scientists from being able to examine only equilibrium or cursory transitional states and from the need for expressing relations in neat closed analytical forms. Numerical integration schemes and the speed of computation have made possible the examination of large systems of differential equations with feedback mechanisms, both from deterministic and stochastic standpoints. Even the simplest self-regenerating population model of Beverton and Holt (1957), which may be regarded as a simulation model in that it has a feedback mechanism, is largely intractable for looking at transitional states and parameter variability without the aid of a computer.

Paulik (1969) gives a good review of simulation modeling in fisheries. He divided the modeling of fishery systems in an admittedly arbitrary way into two categories, management models and scientific models, depending on the manner in which a model is utilized. Management models are employed for decision making in evaluating or planning strategies for management purposes, while scientific models are constructed to help elicit certain basic knowledge of a biological system. The actual implementation of models in the two categories, however, should be similar in utilizing the model for planning, alternative evaluation, organization, and identifying sensitive areas of the system.

There are at least two fishery simulation models currently in existence which were designed to be generally applicable to most exploited populations. The most comprehensive is GAMES (Gales, 1972). This simulator has seven interacting sectors from the fish stock to the marketing of the final fish product, is modular in structure, and uses the most updated means of input/output. Unfortunately, GAMES is still in a state of development. The other simulator, POPSIM, was written by Walters (1969). POPSIM's major feature is an optimization routine for planning harvesting strategies for a number of harvesting periods. Both of these simulation models are easily adapted to the life history characteristics of fish populations which have been traditionally studied in fisheries science. However, the FORTRAN IV computer simulation model, GXPOPS, was written to allow additionally for the life history pattern of many crustaceans and some fishes that require actual copulation in reproduction and a sex-differentiated maturation schedule.

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MODEL STRUCTURE

A flow-chart of GXPOPS indicating the optional life history sectors is presented in Figure 1. Each sector is described by the equations below. The basic time period for calculations in GXPOPS is monthly with all processes summed or averaged annually. There are three output options: 1) annual summaries only, 2) monthly and annual summaries by age class, and 3) monthly listings by age class as well as monthly and annual summaries.

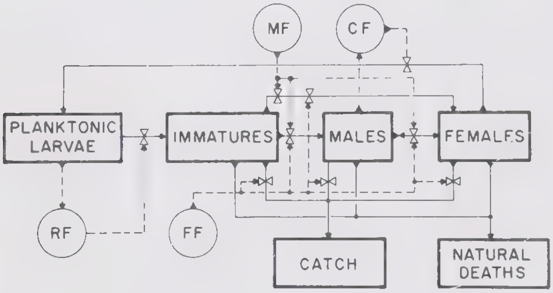

FIGURE 1.—Simplified flow chart of the computer program, GXPOPS. Boxes represent state variable compartments, solid lines represent material flows, dashed lines represent information flows, and circles represent regulatory functions; CF = copulation function, FF = fishing mortality function, MF = sex specific maturation function, and RF = recruitment function.

Mortality

Mortality may be age-specific on a monthly basis and is assumed to be representable by an exponential decline such that

$$N_{i,\,j+1} = N_{ij} e^{-Z_{ij}} \qquad (1)$$

with

$$Z_{ij} = M_{ij} + A_{ij} F_{ij} \qquad (2)$$

where N_{ij} is the number of animals belonging to the ith year class at the beginning of month j, M_{ij} is the instantaneous coefficient of natural mortality, A_{ij} is an availability multiplier, F_{ij} is the potential instantaneous coefficient of fishing mortality of a fully available year class, $i = 1 \ldots n$, and $j = 1 \ldots 12$. With natural and fishing mortality so general one can evaluate the effects of seasonal mortality patterns such as mass winter mortalities, closed seasons, etc. The coefficient A allows patterns of selectivity or seasonal availability, etc. to be incorporated. The average number alive of year class i during month j is given by

$$\bar{N}_{ij} = N_{ij} (1 - e^{-Z_{ij}}) / Z_{ij}. \qquad (3)$$

Growth

The growth in weight of the animals is represented by one of two options, the von Bertalanffy growth equation or a linear segmental growth curve as in POPSIM (Walters, 1969). The von Bertalanffy formulation is

$$w_{ij} = W_\infty \left[1 - e^{-K(12i + j - 13 - t_0)}\right]^3 \qquad (4)$$

where w_{ij} is the average weight of an individual in year class i at the beginning of the month j, and W_∞, K and t_0 are parameters of the von Bertalanffy growth equation. The segmental growth option is formulated as

$$w_{ij} = a + b \, \Delta t \qquad (5)$$

where $a = w_{i,\,j-1}$, $b = (w_{ij} - w_{i,\,j-1})$ and $\Delta t = 1$. Using the segmental option, any shape growth curve may be approximated, including the stepwise growth pattern of crustaceans and many temperate fishes and mollusks.

Yield

Yield is computed monthly both in numbers and weight for each year class under either the von Bertalanffy or linear segmental growth option.

$$Y_{N_{ij}} = A_{ij} F_{ij} \bar{N}_{ij} \qquad (6)$$

where $Y_{N_{ij}}$ is the yield in numbers. Under the von Bertalanffy growth option, the yield in weight, $Y_{w_{ij}}$, is computed as

$$Y_{w_{ij}} = A_{ij}F_{ij}N_{ij}W_\infty \sum_{u=0}^{3} \frac{\Omega_u e^{-uK(12i+j-13-t_0)}}{Z_{ij}+uK}$$

$$x\,[1-e^{-(Z_{ij}+uK)}] \qquad (7)$$

where $\Omega_u = 1, -3, 3, -1$, respectively. With the linear segmental growth option

$$Y_{w_{ij}} = Y_{N_{ij}} \{w_{ij} + (w_{ij+1} - w_{ij})$$

$$[1/Z_{ij} - 1/(e^{Z_{ij}} - 1)]\} \qquad (8)$$

Equations (7) and (8) are modified for monthly calculations from Beverton and Holt's (1957) equations 4.4 and 9.5 respectively.

Maturation

A maturity schedule of the sexes is necessary to compute several relationships associated with the reproductive sextor of GXPOPS. This is accomplished in the simulator with two vectors of age-specific values, one denoting the average fraction of mature males in each year class during the breeding season, ϕ_{mi}, and the other denoting the female fractions, ϕ_{fi}. The mean number of mature males, $\overline{N}_{m_j}$, and mean number of mature females, $\overline{N}_{f_j}$, during month j of the spawning season are

$$\overline{N}_{m_j} = \sum_{i=1}^{n} \phi_{mi} N_{ij} (1-e^{-Z_{ij}})/Z_{ij} \qquad (9)$$

and

$$\overline{N}_{f_j} = \sum_{i=1}^{n} \phi_{fi} N_{ij} (1-e^{-Z_{ij}})/Z_{ij} \qquad (10)$$

with

$$s_j = \overline{N}_{m_j}/\overline{N}_{f_j}, \qquad (11)$$

where s_j is the mean monthly sex ratio. The mean sex ratio for the breeding season is given by

$$\bar{s} = [\sum_{j=t_s}^{t'_s} s_j]/(t'_s - t_s + 1) \qquad (12)$$

where t_s and t'_s are respectively the months that breeding begins and ends.

The maturation fractions, ϕ, are assumed to be constants in the present version of GXPOPS. It is possible that the ϕ may be density-dependent in certain populations. One can investigate the effect of differences in ϕ at equilibrium with the current version of GXPOPS, but it would be a simple matter to reprogram GXPOPS to examine the consequences of any functional hypotheses.

Reproduction

The major components of the reproduction sector of GXPOPS are copulation, egg-carrying (ovigerous period), and hatching. For the common spawing characteristics of freely casting both spermatozoa and eggs, the copulation and ovigerous period sector may be bypassed.

The traditional concept of fertilization success in fisheries population dynamics, excluding the salmonids, is described by Beverton and Holt (1957, p. 61) as:

> . . . if there is free liberation of gametes, with spermatozoa greatly in excess of eggs, and especially if the percentage of successful fertilisations is fairly high, then the number of fertilised eggs would tend to be a constant fraction of the numbers laid. In addition, a large spawning population would tend to distribute eggs over a rather wider area than a small one, so that the number of gametes per unit volume, which in such a situation determines the rate of fertilisation, would not be expected to change much.

Copulation is one mode of ensuring the fertilization of eggs in sexual reproduction. The success of fertilization, therefore, depends on the copulation rate which is at least some function of the sex ratio and density of the mature population. Beverton and Holt recognized this may be the case for a lobster population, in which copulation occurs.

Copulation is a part of reproduction in most commercially exploited crustaceans, and some fishes. With the exception of salmonid studies, where a form of pseudocopulation occurs, population dynamics studies of commercial fisheries have ignored the effects of exploitation on the rate of copulation. Conway (1969) presents the most extensive quantitative treatment of reproduction in insects, whose copulation parallels that of many crustaceans. He recognizes three types of mathematical models for representing reproduction: 1) derivations from the Lotka-Volterra equations, 2) empirical models (essentially multiple regressions from data sets with a number of variables), and 3) structural models of the causal mechanisms likely to be involved.

Derivations from the Lotka-Volterra equations assume that if mating is random, then the rate of change of copulated females is proportional to the expected rate of contact per female times the number of uncopulated females. The rate of contact per female is assumed to be proportional to the number of males, giving

$$dN_f^*/dt = k_c N_m (N_f - N_f^*) \qquad (13)$$

where * denotes copulated females and k_c is the coefficient of copulation. The copulation coefficient may be thought of as consisting of two multipliers — the instantaneous coefficient of males contacting females at random and the fraction of these encounters that result in copulation. Equation 13 has the solution

$$N_f^* = N_f(1 - e^{-k_c N_m}) \qquad (14a)$$

or

$$p = (1 - e^{-k_c N_m}) \qquad (14b)$$

where p is the fraction of mature females that, at the end of the breeding season (scaled to be of one unit length for convenience), have been copulated. Equation (14b) may also be derived probabilistically by assuming the number of copulations is Poisson distributed such that k_c is the mean rate of contact resulting in copulation per male, then

$$P_r\,[x \text{ copulations}] = \varepsilon^{-k_c N_m} \frac{(k_c N_m)^x}{x!}$$

with equation (14b), therefore, expressing the probability that at least one copulation per female has occurred in one unit of time (Klomp, Montfort, and Tammes, 1964 [cited in Conway, 1969]). This assumes that the population is not aggregated but is randomly distributed over the breeding grounds regardless of the size of the population. Philip (1957) has also derived equation (14b) under slightly different circumstances. Writing equation (14a) in terms of the sex ratio (males: females), s, and total mature population, N_a, we have

$$N_f^* = \left(\frac{1}{1+s}\right) N_a \left[1 - e^{-k_c \left(\frac{s}{1+s}\right) N_a}\right]. \qquad (15)$$

Therefore, as the total mature population decreases, or as the sex ratio increases, the number of females being copulated with decrease under this model for reasonable values of s in the virgin state.

With the aid of equation (15) one can easily follow the reasoning of Beverton's and Holt's conclusions for large, long-lived fish populations with essentially a constant sex ratio. The maximum sustainable average yield (MSAY) in these populations is likely to occur at relatively low rates of fishing, hence there would be only a small reduction in population size from the virgin state. If k_c were high, then the reduction in $N_f{*}$ would be negligible. On the other hand, if the population is short-lived, the MSAY is likely to occur at a relatively lower population level. If fishing also increases the sex ratio, the deleterious effects on the size of $N_f{*}$ are compounded.

Equation (13) may be extended to become more realistic for a multiage population under exploitation. Often the mortality during breeding is neglected; however, exploitation may increase the mortality significantly and the breeding season may be protracted. Therefore, with the additional assumption that males make no distinction between year classes of females, for any year class i during month j

$$dN_{fi}^*/dt = k_c N_m(t)\,[N_{fi}(t) - N_{fi}^*(t)\,] - Z_i N_{fi}^* \qquad (16)$$

where

$$N_m(t) = \sum_{i=1}^{n} \phi_{mi} N_{ij} e^{-Z_{ij}t} \qquad (17)$$

and

$$N_{fi}(t) = \sum_{i=1}^{n} \phi_{fi} N_{ij} e^{-Z_{ij}t} \qquad (18)$$

Rewriting equation (16) in terms of the ratio of copulated females to total mature females, *p(t)*, giving

$$dp(t)/dt = k_c \sum_{i=1}^{n} \phi_{mi} N_{ij} e^{-Z_{ij}t}[1 - p(t)], \quad (19)$$

the solution obtained is

$$p_j = [1 - e^{-k_c \sum_{i=1}^{n} \phi_{mi} N_{ij} (1 - e^{-Z_{ij}})/Z_{ij}}] \quad (20)$$

with $t = (0, 1)$ months and $p_0 = 0$. Equation (20) may be further simplified by substitution from equation (9) to give

$$p_j = [1 - e^{-k_c \bar{N}_{mj}}]. \quad (21)$$

Therefore, the fraction of the females in any year class that are copulated is the same for all year classes *provided that* k_c *is not age specific*. Given the fraction copulated in the previous month, p_{j-1} [where $p_{t_s - 1} = 0$], the fraction copulated at the end of the month j is

$$p_j = [1 - (1 - p_{j-1}) e^{-k_c \bar{N}_{mj}}]. \quad (22)$$

The total number of females in the population bearing fertile eggs at the end of the breeding season is then

$$N^{*\prime}_{ft_s} = p_{t'_s} \sum_{i=1}^{n} \phi_{fi} N_{it'_s}, \quad (23)$$

further assuming that one copulation results in fertilization.

Recounting the assumptions implicit in the simple model, equation (23), they are:

1. The instantaneous copulation rate per female is linear and proportional to the number of males.
2. The copulation coefficient is independent of the age of the males and females.
3. The copulation coefficient is independent of population size.
4. A single copulation results in fertilization.
5. Multiple copulations, if they occur, do not alter the fraction of each egg clutch that is fertilized from the first copulation.

In developing a reproduction model for insects, Conway (1969) criticized the first assumption as being unrealistic. Empirical evidence and biological induction suggest that the copulation rate should be concave downwards, rising to a maximum at some intermediate density and declining at very high densities owing to interference. Conway (1969) dismissed the second type of models (empirical) as lacking generality for a critical examination of reproduction, and developed three structural models based on nearest neighbor distances. Given the population size, density, and sex ratio, four parameters are contained in his models as compared with only one for the simple model. Conway fits each of his models to data obtained from the literature on insects. The fits he obtained are hardly remarkable considering that four parameters were estimated, and a number given, for only eight points. However, the fits are an indication of the flexibility and possible validity of Conway's structural concepts—especially since an irregularity in the data with biological significance was predicted with the fitted model. The decline in copulation rate in the data, however, occurs at very high population densities. The major use of GXPOPS will likely be for examining the dynamics of populations under exploitation, hence at less than virgin population densities. Also, since the two data sets given by Conway are adequately described by a straight line for the observations at population densities before the decline in copulation rate occurred, and lacking other empirical evidence to the contrary, equation (22) was adopted as the copulation model in GXPOPS.

Many exploited animals carry their fertilized eggs so that the number of eggs reaching the hatching period is intimately tied to the survival of the females during the ovigerous period. If it is assumed that all female mortality results in the loss of the eggs as well, then the number of copulated females reaching the hatching period is given by

$$N^{*\prime}_{ft_h} = p_{t'_s} \sum_{i=1}^{n} \phi_{fi} N_{it_h} \quad (24)$$

where t_h is the time at hatching. Instantaneous hatching is assumed, so t_h represents the mean hatching time.

Individual fecundity (eggs per female) is usually correlated with the size of the individual. Many plots of fecundity on length appear to be concave upward, which indicates that fecundity is closely proportional to the weight of the individual. In order to be more useful generally, however, fecundity in GXPOPS is represented by a vector of mean viable eggs per female at hatching by age class, λ_i, such that the total number of larvae hatched, L_h, is given by

$$L_h = p_{t'_s} \sum_{i=1}^{n} \lambda_i \phi_{f_i} N_{it_h}. \qquad (25)$$

Recruitment

Any equilibrium point achieved with the population model as now formulated is likely to be unstable, such that with a sustained increase or decrease in mortality the population will decrease to extinction or increase to infinite size. Most successful natural populations are believed to achieve equilibrium through any of a number of homeostatic mechanisms associated with density-dependent reproduction or mortality. One such mechanism already mentioned is a decrease in copulation rate at high densities. Others include a lack or destruction of oviposition sites at high densities as in insects or salmonid fishes, an overutilization or competition for a fixed food supply, cannibalism, predator-prey interactions, etc. The usual mode of population regulation assumed in fisheries studies is through density-dependent early stage (or larval) mortality. Treatises on this subject can be found in Ricker (1954, 1958) and Beverton and Holt (1957).

Two models have been widely used in fishery population dynamics; GXPOPS allows the selection of one or the other. The first model, owing to Beverton and Holt (1957), states that the simplest assumption one can make is that the larval mortality coefficient can be expressed as a simple linear function of larval population size

$$dL_t/dt = -(\mu_1 + \mu_2 L_t)\, L_t \qquad (26)$$

where μ_1 and μ_2 are the density-independent and density-dependent larval mortality coefficients. Equation (26) integrates to

$$L_j = [\mu_2/\mu_1\, (e^{\mu_1} - 1) + e^{\mu_1}/L_{j-1}]^{-1} \qquad (27)$$

for the survival of larvae from month j - 1 to j. Collecting the constants we have

$$L_j = 1/(\alpha_1 + \alpha_2/L_{j-1}),$$

or

$$L_{h+t_r} = 1/(\alpha_1 \sum_{r=0}^{t_r-1} \alpha_2^r + \alpha_2^{t_r}/L_h) \qquad (28)$$

for t_r months of larval existence. Equation (28) is a concave downward function that increases monotonically with L_j for a constant period of larval existence and it approaches an asymptote of $\sum_{r=0}^{t_r-1} \alpha_2^r/\alpha_1$ at an increasing rate as α_2 increases.

The second model, owing to Ricker (1954, 1958), simply assumes that the density-dependent coefficient, μ_2, may operate only until some critical size is reached and that the time to attain this critical size may be proportional to the size of the larval population at hatching, L_h, which gives

$$dL_t/dt = -(\mu_1 + \mu_2 L_h) L_t$$

or on integrating

$$L_{h+t_r} = L_h e^{-(\mu_1 t_r + \mu_2 L_h)} \qquad (29)$$

for t_r months of larval existence. Equation (29) is also concave downwards, but monotonically increases to a maximum at $L_h = 1/\mu_2$, and then monotonically decreases approaching zero as L_h becomes infinite.

Both equations (28) and (29) allow a population to achieve stability over a range of sustained mortality rates. Equation (29), additionally, will produce oscillations in the population (Beverton and Holt, 1957), the criteria for which are given by Paulik and Greenough (1966).

Constant recruitment of size $1/\alpha_1$ may be simulated with GXPOPS by selecting equation (28) and setting $\alpha_2 = 0$.

Timing in the Simulator

Reference in this study is made to a year divided into 12 mo because the reproductive cycles of many exploited fish populations are annual. It is just as easy to consider the "year" as a reproductive cycle (16 days, 3 yr, etc.) divided into 12 time periods of equal length.

The conventional notation, for numbering timestream entities, is for the initial or first instance to be denoted as 0. The computer, however, begins with 1 in executing "DO" loops, etc., therefore, the ordinal numbering system is used in GXPOPS. The first month and year are denoted as 1, as are the initial numbers and yields of the first month and year, and the young of the year. The simulator takes the hatching time, t_h, as time 1 (i.e., $L_h = L_1$) and the year is carried on a biological fiscal basis. For example, if hatching occurs on April 1, recruitment to the main population on July 1 of the first year of life, and breeding begins October 1 and ends December 1; then

$$t_h = 1,\ t_r = 3,\ t_s = 7, \text{ and } t_s' = 8,$$

respectively. If recruitment does not occur until July 1 of the third year of life, then $t_r = 27$.

EXAMPLE: A PANDALID SHRIMP POPULATION

GXPOPS was designed to be useful for examining the responses of many life history patterns to exploitation. The impetus, however, was to examine the response to exploitation of a pandalid shrimp life history (Fox, 1972). Pandalid shrimps are protandric hermaphrodites—i.e., individuals mature as males but later transform to function as females (Berkeley, 1930), fertilization is accomplished through copulation, the females carry fertilized eggs 3-9 mo until hatching, and they exhibit pronounced stepwise growth. While the extensive simulation studies investigating the effects and management implications of all sectors of the pandalid shrimp model will be published subsequently, one particular study of the effect of season length on the simulated fishery is useful for illustrating the utility of GXPOPS.

Table 1 contains the parameters of the simulated pandalid shrimp population which 1) consists of six year classes, 2) is fully recruited to the fishable population during the third year of life (at 2 yr old), 3) breeds over 2 mo, 4) carries its eggs 5½ mo until hatching, 5) recruits to the main population during the fourth month of life (3 mo after hatching), 6) matures as males during the third year of life (at 2 yr old), and 7) transforms into females during the fourth year of life (at 3 yr old). The stepwise growth in weight is given in Figure 2.

Exploiting the simulated pandalid shrimp produced the relationship between equilibrium yield and fishing effort (= instantaneous fishing mortality coefficient since the catchability coefficient was assumed to be 1.0) given in Figure 3. An equilibrium yield was achieved with fishing effort up to 1.4, with the maximum equilibrium yield occurring at about 1.0. Fishing above a level of 1.4 did not result in equilibrium within 25 yr of simulated fishing, and continued fishing somewhere between 1.4 and 2.0 would eventually result in extinguishing the population. By not including the effect of random mating (copulation), i.e., $k_c = \infty$, the simulated population achieved equilibrium out to nearly $F = 1.8$ (Fox, 1972). This exhibits some need for considering the implications of copulation success in evaluating management alternatives.

The equilibrium yields given in Figure 3 are for an annual pandalid shrimp fishery. Several states, however, have closed seasons during that part of the year when females are carrying fertilized eggs — ovigerous period — (Dahlstrom, 1970). For the simulated pandalid shrimp population, the ovigerous period lasts 6 mo (months 7-12). It is of interest to compare the results of the closed ovigerous season strategy with other possible season lengths, all beginning subsequent to hatching and running continuously until reaching the closed season.

TABLE 1.—Parameters of the simulated pandalid shrimp population.

Parameter	Symbol	Value
1. Number of year classes	n	6 (i = 1-6)
2. Instantaneous natural mortality coefficient	M_{ij}	0.06 (for all i and j)
3. Availability multipliers	A_{ij}	0.0 (for $i < 3$) 1.0 (for $i \geqslant 3$)
4. Month breeding begins	t_s	7
5. Month breeding ends	t_s'	8
6. Year of first maturity	t_m	3
7. Age (mo) at first recruitment	$t_r + 1$	4
8. Copulation coefficient	k_c	10^{-9}
9. Recruitment parameters of the Beverton and Holt model	α_1 α_2	3.2851×10^{-11} 1.01
10. Fecundity coefficients	λ_i	0.0 (for i = 1-3) 1314 (for i = 4) 1679 (for i = 5) 1997 (for i = 6)
11. Male maturity fractions	ϕ_{mi}	0.0 for i = 1, 2 and 4-6 1.0 for i = 3
12. Female maturity fractions	ϕ_{fi}	0.0 for i = 1-3 1.0 for i = 4-6

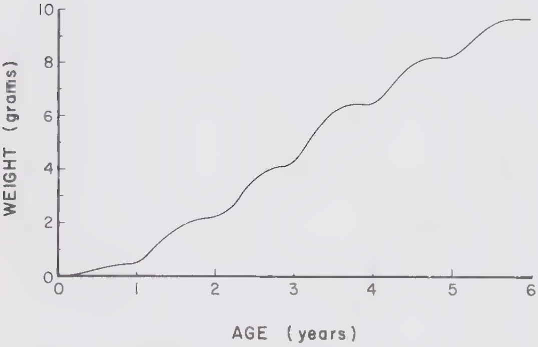

FIGURE 2.—Arbitrary growth curve exhibiting the stepwise growth pattern of pandalid shrimps.

The simulated pandalid shrimp population was fished for six different season lengths, from 12 to 2 mo after the hatching period (Table 2). The maximum equilibrium yield for each season length occurred with an *annual* fishing mortality coefficient, *F*, of 1.0. This means that the monthly fishing effort must increase proportionally to the inverse of the season length to obtain the maximum equilibrium yield (column 2, Table 2). Of those seasons simulated, the greatest equilibrium yield and catch per unit effort were obtained with the 8-mo season (columns 3 and 4, Table 2). Compared with an annual fishery, however, the 8-mo season resulted in a 5% decrease in the average weight of a shrimp in the catch (column 5, Table 2). The 6-mo season (closure during the breeding, ovigerous, and hatching periods) was only slightly less than the 8-mo season in yield and catch per unit effort, but it was better than the annual fishery. However, there was an 11%

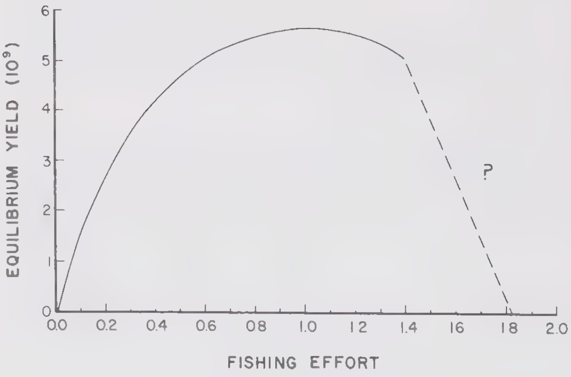

FIGURE 3.—Relationship between equilibrium yield and fishing effort for the simulated pandalid shrimp population. Dashed line represents nonequilibrium region.

TABLE 2.—Effect of season length, beginning subsequent to hatching, on maximum equilibrium yield and allied fishery parameters for the simulated pandalid shrimp population.

(1) Season length (months)	(2) Monthly fishing effort	(3) Season yield in weight	(4) Average monthly catch/effort	(5) Average individual weight	(6) Breeding success (percent)
12	1.0	5.60×10^9	0.467×10^9	3.7	85.5
10	1.2	5.68×10^9	0.474×10^9	3.6	82.0
8	1.5	5.70×10^9	0.475×10^9	3.5	76.1
6	2.0	5.67×10^9	0.472×10^9	3.3	71.3
4	3.0	5.63×10^9	0.469×10^9	3.1	71.3
2	6.0	5.57×10^9	0.464×10^9	2.9	71.3

decrease in average weight as compared to the annual fishery. The breeding success, defined as the fraction of available eggs which are fertilized, declined with the season length until a 6-mo season was reached.

An unknown factor not programmed into the simulation model, however, is the effect of trawling on the behavior of the shrimp during breeding or on the possibility of causing dislodgement of the egg clutches and a subsequent higher mortality rate. In view of these uncertainties, the adoption of a 6-mo season from hatching to the onset of breeding, as several states have, appears to be a biologically prudent approach for a natural population similar to the simulated population. The 6-mo season is only slightly lower in maximum equilibrium yield, catch per unit effort, and average size than the optimal 8-mo season, but is better than the annual fishery in the first two categories. The actual implementation of a 6-mo season on an annual fishery, however, would have to weigh socioeconomic factors because the maximum yield is obtained with twice the amount of fishing effort per month as compared with the annual season. If the fishery were only able, at the time of adopting the closed season, to exert a monthly effort of 1.0, the expected seasonal equilibrium yield is about 10-15% less than that for the annual fishery, but the expected equilibrium mean monthly catch per unit effort would increase 70-80%. The latter should provide a substantial increase in the economic standard of an average fisherman, provided that he has an alternative means of investment for the 6-mo closed season which would provide a sufficient return. The simulation model can be used also to evaluate the expected transitional states from an annual fishery to a seasonal closure fishery as well as the expected equilibrium results discussed here. A socioeconomically feasible strategy, then, may be determined given the current state of the fishery.

PROGRAM AVAILABILITY

A listing and card set-up documentation for program GXPOPS are available on request from the author.

ACKNOWLEDGMENTS

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A Review of the Literature on the Development of Skipjack Tuna Fisheries in the Central and Western Pacific Ocean

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ABSTRACT

There has been a rapid acceleration in efforts to develop skipjack tuna fisheries in the central and western Pacific. This is because the resources of the larger tunas (yellowfin, bigeye, bluefin, and albacore) are already being fished at or near the maximum sustainable level. The greatest potential for increased harvest appears to be the skipjack resource. To assist the skipjack development effort, pertinent information on the subject is summarized and a bibliography of selected references is included.

INTRODUCTION

The rapid acceleration of interest in skipjack tuna, *Katsuwonus pelamis*, fishery development in the central and western Pacific has prompted several exploratory fishing operations in the area beginning in 1971. To aid the development of skipjack tuna fisheries we thought that a review of the literature and a compilation of a bibliography on earlier developmental work would be useful. Most of these references are available in any reasonably large research library or in most fisheries libraries. All are available in the library of the Honolulu Laboratory of the Southwest Fisheries Center or in its archives and files. Many references dealing with the subject have been omitted, no doubt some through oversight but chiefly because they are incorporated in other documents in our bibliography.

The development of a fishery, from the discovery of the resource to the time that full production is reached, can be diagramed. Figure 1 is a convenient diagram for considering the development of a skipjack fishery in the central and western Pacific. The diagram is complicated by the fact that one of the methods widely used in capturing skipjack tuna requires live bait. Thus we have a fishing method dependent upon another fishery, and it is desirable to consider the development of a fishery for the bait species along with that for skipjack. Hence, a parallel flow chart for the baitfish fishery is included and pertinent references are incorporated.

There is less literature on the baitfishes used for skipjack fishing in the central and western Pacific than there is on the skipjack. Only in three areas is systematic collection of baitfish information under way, these being Palau, Hawaii, and American Samoa. In both Palau and Hawaii, where substantial skipjack fishing is carried out, baiting records are available for several years, and some research has been or is being conducted to provide a better understanding of the biology and management of the bait resources.

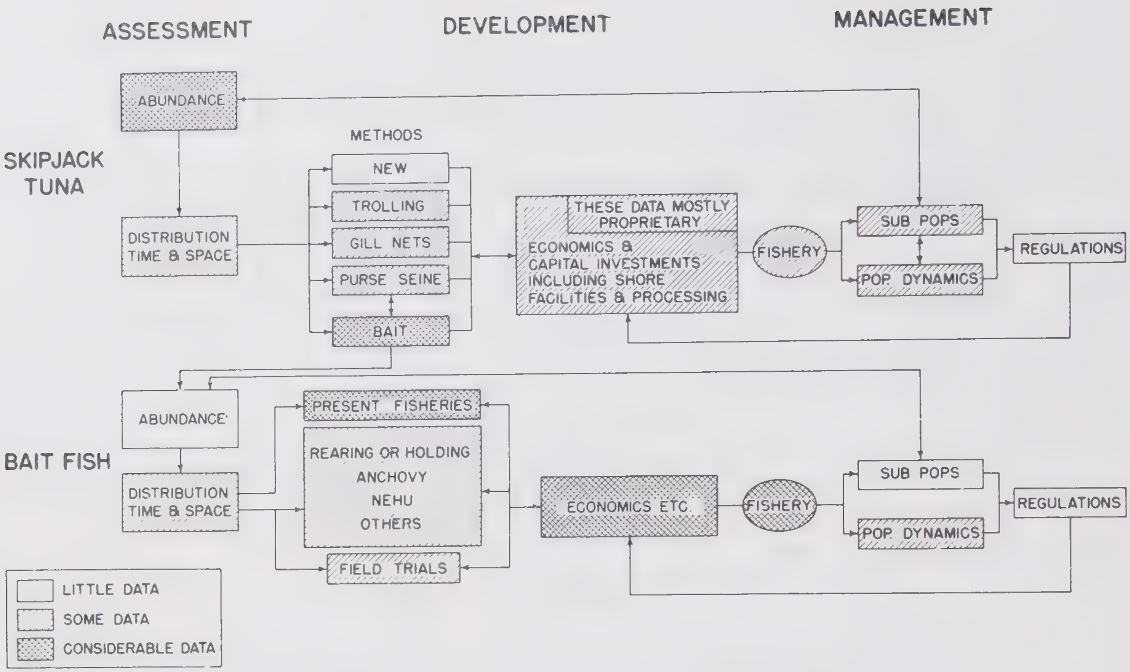
ASSESSMENT
DEVELOPMENT
MANAGEMENT
SKIPJACK TUNA
ABUNDANCE
DISTRIBUTION TIME & SPACE
METHODS
NEW
TROLLING
GILL NETS
PURSE SEINE
BAIT
THESE DATA MOSTLY PROPRIETARY
ECONOMICS & CAPITAL INVESTMENTS INCLUDING SHORE FACILITIES & PROCESSING
FISHERY
SUB POPS
POP. DYNAMICS
REGULATIONS
BAIT FISH
ABUNDANCE
DISTRIBUTION TIME & SPACE
PRESENT FISHERIES
REARING OR HOLDING
ANCHOVY
NEHU
OTHERS
FIELD TRIALS
ECONOMICS ETC.
FISHERY
SUB POPS
POP. DYNAMICS
REGULATIONS
LITTLE DATA
SOME DATA
CONSIDERABLE DATA

Figure 1. — Flow diagram for the development of skipjack fisheries in the central and western Pacific.

SKIPJACK FISHERY ASSESSMENT

Abundance

We will consider those references that attempt to quantify the potential yield of skipjack from the central and western Pacific. These fall generally into three categories: (1) papers and reports coming from Japanese workers, who have concentrated primarily on fisheries near Japan and in the southwestern (south of lat 24°N, west of long 160°E) Pacific, (2) papers originating with the Honolulu Laboratory, and (3) papers from the west coast of the United States, chiefly from the Inter-American Tropical Tuna Commission (IATTC).

The Japanese workers have estimated the potential yield of skipjack in the Pacific in a number of ways based upon current and prewar production and distributional records from their fishing fleet. Estimates for the western Pacific made several years ago include 30,000 metric tons for the Caroline Islands, 15,000 metric tons for Palau (Uchida, 1970), and 150,000-200,000 metric tons for the Japanese home island and Ryukyu Islands fishery (based on peak landings). No estimates were found for the potential of the New Guinea and Coral Sea grounds, but recently Japanese estimates as high as 1.5-2.0 million tons for the entire Pacific have been made ([U.S.] Bureau of Commercial Fisheries, 1970a; U.S. National Marine Fisheries Service, 1971).

In the eastern Pacific the IATTC workers (Shimada and Schaefer, 1956; Calkins, 1961; Broadhead and Barrett, 1964; Joseph and Calkins, 1969) have suggested that (1) a considerable tonnage of skipjack are either unexploited or never enter the eastern Pacific fishery, and are located somewhere west of long 120°W, and (2) present landings (ca. 50,000 metric tons) could safely be increased and perhaps doubled.

Workers at the Honolulu Laboratory, particularly Rothschild (1966), Silliman (1966), and Rothschild and Uchida (1968), also concluded that there is a large potential yield of skipjack tuna in the central Pacific, their estimates ranging from some 40,000 to over 200,000 metric tons on a maximum sustainable yield basis.

Although all the conclusions are highly

speculative, it is reasonable to assume that the potential yield of skipjack in the central and western Pacific has not been reached and that the resource is large enough for a sizable expansion of the fishery.

Distribution in Time and Space

Our knowledge of skipjack distribution comes primarily from the established fisheries in the eastern Pacific, Hawaii, French Polynesia, and the western Pacific, as reported by a number of workers including Imamura (1949), Shimada (1958), Shippen (1961), Calkins and Chatwin (1967), Brun and Klawe (1968), Isa (in press), and Tohoku Regional Fisheries Research Laboratory (n.d.). Supplementing this information are incidental catches of skipjack taken from tuna longline records (Kasahara, 1968; Miyake, 1968). Records are also available from research and exploratory vessels scouting for skipjack (Smith, 1947; Smith and Schaefer, 1949; Royce and Otsu, 1955; Yoshida, 1960; McKenzie, 1961; Waldron, 1964; York, 1969; Hida, 1970a, b). Currently an FAO development project has been initiated in Fiji, and new fisheries established in the Solomons and New Guinea area are beginning to provide information from the southwestern Pacific.

Tag recoveries are beginning to contribute to the understanding of the migration and seasonal occurrence of skipjack (Rothschild, 1965; Fink and Bayliff, 1970; Kasahara et al., 1971). From such observations several summaries on their occurrence have been published. These include [U.S.] Bureau of Commercial Fisheries (1963), Kawasaki (1965), Kasahara (1968), Rothschild and Uchida (1968), and Kasahara et al. (1971). These summaries led to hypotheses on the origin and migration of skipjack in the Pacific, including those by Rothschild (1965), Naganuma (in Kasahara, 1968), and Matsumoto[1].

Following the formulation of distributional and migration hypotheses, some attempts have been made to generalize the distribution of the skipjack and to relate them to their environment. In the eastern Pacific, their north-south distribution is believed to be limited between surface isotherms of 20° and 29°C (Williams, 1969). In the central Pacific various attempts have been made to describe the relation of skipjack distribution to the various current systems (Seckel and Waldron, 1960; Seckel, 1963) and in the western Pacific to seasonal changes in water temperature and current systems (Inanami, 1941; Kawasaki, 1965). For the central and western Pacific, the general pattern is one of a northward expansion from near equatorial waters as the summer season progresses and a contraction to the lower latitudes with the onset of fall and winter. The seasonal shift can best be seen in reports by Kasahara (1968) and the Tohoku Regional Fisheries Research Laboratory (n.d.).

SKIPJACK FISHERY DEVELOPMENT

Methods

Until recently pole-and-line fishing with live bait accounted for most of the skipjack landings. Recently purse seining has begun to produce an increasingly significant fraction of the catch. These two methods have greatly exceeded the small amounts taken by trolling and with gill nets. Trolling is generally limited to nearshore, small-boat subsistence fisheries and by research vessels. In French Polynesia, however, this method has been developed into a fairly productive fishery (Van Campen, 1953; Van Pel and Devambez, 1957; Brun and Klawe, 1968). Some estimates of potential production by trolling can be obtained from survey reports such as Smith (1947), Smith and Schaefer (1949), Bates (1950), Welsh (1950), Murphy and Ikehara (1955), and Iversen and Yoshida (1957).

As with trolling, gillnetting until recently has been limited to scientific surveys as an indicator of the distributions of tunas (Matsumoto, 1952; Shomura, 1963). In the last decade gillnetting for tunas has been developed commercially in Australia and New Zealand (Temple, 1963; York, 1969; Avery, 1970).

Purse seining is the preferred method for taking tunas in the eastern Pacific, where in 1971 approximately 100,000 metric tons of skipjack were taken. A review of this method is given by McNeely (1961) and Green and Perrin (1970). In the central Pacific purse seining has been tried on a few occasions in Hawaiian waters (Murphy and Niska, 1953). The method has shown some promise ([U.S.] Bureau of Commerical Fisheries, 1969a) and recently another attempt (Hawaii. Fish and Game and Bumble Bee Seafoods, 1970) has taken place with partial success. In the western Pacific the Japanese have been increasing their experimental and exploratory purse seine work, which is summarized by Watakabe (1970). Like the Hawaiian experiments, these efforts have not been an unqualified success. American west coast purse seiners have also made some excursions into the western Pacific with mixed success ([U.S.] Bureau of Commercial Fisheries, 1970b). Numerous reasons have been cited for the difficulties encountered in applying this method of fishing in the central and western Pacific, chief among these being the greater depth of the thermocline and the clearer waters in the tropics. This method may yet become increasingly important following development work involving gear modifications and specialized techniques.

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[1] Matsumoto, W.M. Distribution, relative abundance and movement of skipjack tuna (*Katsuwonus pelamis*) in the Pacific Ocean based on Japanese tuna longline catches, 1964-67. Unpublished manuscript filed at National Marine Fisheries Service, Southwest Fisheries Center, Honolulu Laboratory, Honolulu, Hawaii 96812.

Pole-and-line fishing with live bait is still the preferred method in the central and western Pacific. There are many references to live-bait fishing in these areas from prewar years (Ikebe and Matsumoto, 1937; Matsumoto, 1937; South Seas Government-General, 1937a, b, c; Watanabe, 1940; Ikebe, 1941) and numerous reports from after the war including June (1951b), Inoue (1966), Hida (1970b), and Uchida (1970).

Little has been published on new methods (Alverson and Wilimovsky, 1964; Kristjonsson, 1968). Some work has been done on improved purse seining (Green, Jurkovich, and Petrich, 1970) and purse seining in combination with live bait (Hawaii. Fish and Game and Bumble Bee Seafoods, 1970).

Attracting and concentrating fish under floating objects (Gooding and Magnuson, 1967; Hunter and Mitchell, 1968) and electro-fishing (Tester, 1959) are other methods that have been tried or suggested. Recently the Japanese have developed an automatic skipjack fishing device which shows considerable promise (Suzuki Tekkojo Kabushiki Kaisha, 1970) and the Tahitian troll-pole method (Van Campen, 1953), though not new, is a method that may well prove applicable to other areas.

Economics and Capital Investment

Most of the information on cost and investment economics is from industry, and the data are proprietary and can only be obtained by special arrangement with the appropriate companies. Some information on the importance of skipjack fishery development for the western Pacific is included in the Nathan Report (Nathan Associates, 1966), in [U.S.] Bureau of Commercial Fisheries (1969a), and in Pacific Islands Development Commission (1971). Shang (1969) discusses the economic aspects of the Hawaiian skipjack fishery. Production figures are generally available from a number of sources including IATTC, the National Marine Fisheries Service, the State of Hawaii, and the Japan Fisheries Agency.

FAO summarizes these statistics annually in its Yearbook of Fishery Statistics (Food and Agriculture Organization of the United Nations, 1970). These are generally several years late and do not reflect the rapid changes that are occurring. Because of the proprietary nature of the data, the production figures often are pooled for a large geographical area so it is impossible to tell how many fish are landed from any one location.

SKIPJACK FISHERY MANAGEMENT

With the rapid expansion of the skipjack fishery, conservation and management of the resource should be of concern to all interests. At present there is no convention to manage and protect the tunas of the central and western Pacific.

Management requires certain broad items of information. The first is whether or not a fishery exploits a single stock or several more or less independent stocks or subpopulations. Generally the skipjack population is believed to be separated into a western Pacific stock that ranges from the Philippine Sea to the home islands of Japan and from the Ryukyus south to New Guinea and into the Coral Sea, and a central Pacific stock that probably extends from the Carolines and the eastern side of the Marianas all the way to the Americas. This theory is supported by genetic evidence summarized by Fujino (1967, 1970a, b, in press) by morphometrics (Kawasaki, 1955a, b, 1964), and by tagging (Otsu, 1970; Kasahara et al., 1971).

The second factor in the management of the skipjack is the dynamics of the exploited population. Sources of data on the population dynamics of skipjack are listed in the bibliography (Tauchi, 1943; Shimada and Schaefer, 1956; Kawasaki, 1964, 1965; Fink, 1965; Rothschild, 1965, 1966; Silliman, 1966; Joseph and Calkins, 1969; Joseph, 1970). Because the fisheries we are concerned with are in the developmental stage, there has been no concerted effort toward the development of a management plan for these fisheries. None of these references deals specifically with management.

BAIT FISHERY ASSESSMENT

Abundance

There is little published data on the quantitative abundance of baitfishes in the central and western Pacific. The majority of the available work has been done on the Hawaiian anchovy, or nehu, *Stolephorus purpureus* (Tester, 1951, 1955; Bachman, 1963; Au, 1965). Investigations are currently underway on the abundance and population dynamics of the Palauan anchovy, *Stolephorus heterolobus*, by Garth Murphy and his group at the University of Hawaii. In addition, there are some notes on the biology of the Marquesan sardine, *Sardinella marquesensis*, (Nakamura and Wilson, 1970) which may have some bearing on a similar species that occurs in the Eastern Carolines, Marshall Islands, Fiji, and elsewhere. This study suggests that the Marquesan sardine cannot withstand extensive fishing pressure. Ikebe and Matsumoto (1938) made some estimates of bait resources near Saipan. Few species and small populations were reported and special fishing techniques were required to take them.

Distribution in Time and Space

Apart from estimates of abundance based on quantitative analysis, a great deal of work has been done to locate suitable bait species by search and sampling in areas where these fishes are needed to support tuna fisheries. Reports of bait surveys include translations from Japanese investigations ranging from prewar investigations in the waters of Ponape and Palau (South Seas Government—General, 1937a, c), Loliai, Lamotrek, and Puluwat (Matsumoto, 1937) to the recent (Kikawa, 1971) report on baitfish surveys in the New Guinea area.

There are reports in English from several areas. For Hawaii and the Leeward Islands there are June (1951a), Tester (1951), Hida and Morris (1963), Au (1965), and Nakamura (1970). For the Micronesian area and the central Pacific, there are Ikehara (1953) and June and Reintjes (1953) on the baitfishes of the central Pacific and Wilson (1971) on the baitfishes in Truk. Still being prepared is a paper by Wilson[2] covering live bait in the Palaus. In addition is the report by Hida (1971) on the current National Marine Fisheries Service investigations in the Trust Territory. There is some unpublished material on baitfishes in Samoa (Swerdloff[3]); a paper by Royce (1954) covering the Marquesas and Tuamotus; and finally papers by Hida and Thomson (1962) covering the introduction of threadfin shad, *Dorosoma petenense*, and Hida and Morris (1963) reporting on the introduction of the Marquesan sardine into Hawaii.

BAIT FISHERY DEVELOPMENT

Present Fisheries

With regard to present fisheries for bait, there is no current report available on any of the important bait species, except Bachman (1963). However, catch and effort statistics are maintained both in Hawaii and Palau and reports of the current status of these fisheries can be obtained from the appropriate Fish and Game and Marine Resources Departments.

Rearing or Holding

From time to time attempts have been made to improve the availability of bait by supplementing the natural supply with bait held in pens or reared in ponds.

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[2] Wilson, P. T. Observations of various tuna bait species and their habitat in the Palau Islands. Division Headquarters, Trust Territory of the Pacific Islands, Koror, Palau, Western Caroline Islands 96940.

[3] Stanley N. Swerdloff, Director, Office of Marine Resources, Government of American Samoa, Pago Pago, American Samoa 96920.

Anchovy.—The success of the Japanese southern waters fishery depends upon the transportation of live bait from the home islands of Japan to as far south as the equator (Iwasaki, 1970; Anonymous, 1971). Similar efforts have been made in Hawaiian waters with the transportation of west coast anchovy in 1932 (Brock, 1960). In 1971, an additional attempt was made to bring anchovies from California to Hawaii. More than 100 buckets (1 bucket ≈ 8 lb.) of the northern anchovy, *Engraulis mordax*, were brought from San Diego, Calif., to Honolulu aboard a bait boat with better than 80% survival after 15 days. The problems of mortality do not appear to be great and the cost of transportation for large quantities of bait may be economically feasible.

Nehu.—A number of attempts have been made to improve the keeping of nehu aboard vessels (Hiatt, 1951; Pritchard, 1953; Burdick, 1969; Baldwin, 1970; Baldwin, Struhsaker, and Akiyama, 1971). The handling of nehu for better survival is summarized by Baldwin (1969) and Baldwin et al. (1971). There is also a report on development of a separate baitfish holding facility for nehu ([U.S.] Bureau of Commercial Fisheries, 1969b).

Others.—Studies also have been made on rearing introduced species as substitutes for native baitfishes. These species include the threadfin shad (Iversen and Puffinburger)[4] and tilapia, *Tilapia mossambica* (Brock and Takata, 1955; King and Wilson, 1957; Hida, Harada, and King, 1962; Uchida and King, 1962). Marquesan sardine were introduced into Hawaii in 1961 and are established but not in sufficient quantity for bait fishing (Hida and Morris, 1963).

Field Trials

There have been several experiments designed to improve the effectiveness of natural live bait, as well as tests of new live bait species. Tests of the natural baits are reported in Welsh (1949) and Yuen (1959, 1969). Tests conducted using tilapia as an alternate bait for skipjack in Hawaii are reported by Shomura (1964). A report of recent trials using threadfin shad as live bait in Hawaiian waters is given by Iversen (1971).

Economics and Capital Investment

Studies were conducted to determine the value of live bait to the tuna fishermen in order to explore the economics of supplying live bait to tuna vessels. Some estimates of the value of nehu to fishermen and a breakdown on the probable production costs for threadfin shad as a live bait are reported by Shang and Iversen (1971). Brock and Takata (1955) also provided an estimate of the value of nehu to Hawaiian fishermen.

BAIT FISHERY MANAGEMENT

Some work on the problem of defining subpopulations of live bait species has been done in Hawaii. Matsui (1963) reports on populations of nehu in the vicinity of Maui, Strasburg (1960) reports on the discovery of an offshore species of nehu, and Tester and Hiatt (1952) report on variations in meristic characters in the nehu.

Management of baitfishes in the central and western Pacific has not been implemented. There is, however, some information on the population dynamics of these fishes. Bachman's (1963) thesis considers fluctuations and trends in the abundance of nehu for Hawaii. The present study by Murphy, University of Hawaii, in Palau is the only current investigation in the population dynamics of a baitfish. However, the National Marine Fisheries Service is beginning to study the biology of the sardine in the Marshall Islands. The Fisheries Departments of the Government of American Samoa and the Trust Territory of the Pacific Islands are collecting or will collect fishery and biological data from their baiting grounds for future management investigations.

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FOOD OF TUNAS AND DOLPHINS (PISCES: SCOMBRIDAE AND CORYPHAENIDAE) WITH EMPHASIS ON THE DISTRIBUTION AND BIOLOGY OF THEIR PREY *STOLEPHORUS BUCCANEERI* (ENGRAULIDAE)

Thomas S. Hida[1]

ABSTRACT

The results of examining the stomach contents of skipjack tuna (*Katsuwonus pelamis*), bigeye tuna (*Thunnus obesus*), yellowfin tuna (*Thunnus albacares*), kawakawa (*Euthynnus affinis*), common dolphin (*Coryphaena hippurus*), and the little dolphin (*Coryphaena equiselis*) caught by live bait pole-and-line fishing and trolling in the equatorial eastern Pacific and around the Samoa Islands are presented. Fishes, crustaceans, and molluscs were found to be important food items. The presence of the anchovy, *Stolephorus buccaneeri*, among the stomach contents was of particular interest, and information gained on their distribution, size frequency, fecundity, and food habits is presented.

This report is based mainly on observations and stomach sample collections that were made during *Charles H. Gilbert* cruise 116 to the equatorial eastern Pacific in October-November 1969 (Hida, 1970a) and cruise 117 to the Samoa Islands in February-April 1970 (Hida, 1970b). In this study, *Stolephorus buccaneeri* was first found in the stomach contents of bigeye and skipjack tunas caught in the equatorial eastern Pacific and again in the stomach contents of tunas caught around the Samoa Islands. Since there has been no food study made of tunas and dolphins from these areas and very few reports on the distribution and biology of *S. buccaneeri,* it is the intent of this paper to (1) describe the food items of the tunas and dolphins caught in these two geographically distant and environmentally diverse—oceanic versus insular—areas, (2) extend the known distributional range of *S. buccaneeri,* (3) report on biological information obtained from the anchovy specimens. *Charles H. Gilbert* is a U.S. Department of Commerce, NOAA research vessel assigned to the Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service. Objectives of the cruises were to assess the distribution and abundance of surface swimming tunas, to tag and release skipjack tuna (*Katsuwonus pelamis*) and yellowfin tuna (*Thunnus albacares*) for migration and growth studies, and to collect blood samples of these tunas for subpopulation studies. Tunas and dolphins were caught by live bait pole-and-line fishing and by trolling. Threadfin shad, *Dorosoma petenense*, were transported from Honolulu in baitwells on both cruises and used as chum for the fishing operation. It was the exclusive baitfish used on cruise 116, while on cruise 117 supplementary baitfishes, mostly sardines, *Sardinella melanura* and *Herklotsichthys punctatus*, and a mackerel, *Rastrelliger kanagurta,* were caught in Pago Pago Harbor and used. Since anchovies were not used as live bait on either cruise, the occurrence of *S. buccaneeri* in the stomachs of the tunas examined indicates that this species is a natural food item in this area.

Many studies have been made on the food and feeding habits of tunas in the Pacific. Ronquillo (1953) examined the stomach contents of yellowfin tuna, skipjack tuna, kawakawa (*Euthynnus affinis*), and the common dolphin (*Coryphaena hippurus*) caught in Philippine seas.

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He found that juvenile fish, especially the acronurus larvae of Acanthuridae, were most important in their diet. Also of importance were members of the fish families Trichiuridae, Scombridae, Triacanthidae, Holocentridae, Balistidae, and Monacanthidae, and invertebrates such as squids, larval and juvenile stomatopods, larval crabs and shrimp. Hotta and Ogawa (1955) examined the stomach contents of skipjack tuna caught to the east and south of the main Japanese islands and reported that Scombridae, Engraulidae, Exocoetidae, and Holocentridae were major dietary items. Important invertebrates included squids, crab larvae, euphausiids, and shrimp. Alverson (1963) examined the stomach contents of skipjack and yellowfin tunas caught in the eastern tropical Pacific. He found euphausiids to be the main food items for skipjack tuna, followed by Gonostomatidae, Exocoetiidae, and the "red crab," *Pleuroncodes planipes*; and for yellowfin tuna, the "red crab," the swimming crab (Portunidae), Thunnidae, Ostracidae, Exocoetidae, and Tetraodontidae. Waldron and King (1963) studied the stomach contents of skipjack tuna taken around the Hawaiian, Line, and Phoenix Islands and found that common dietary items were Gempylidae, Scombridae, Mullidae, Chaetodontidae, and Holocentridae. Larval and juvenile skipjack tuna, stomatopod larvae, shrimp, and crab megalops were also important. E. Nakamura (1965), upon examination of the stomach contents of skipjack tuna from the Marquesas and Tuamotu Islands, reported that scombrids, with skipjack tuna constituting a high percentage, were common food items. Serranidae, Lutjanidae, and Gempylidae were of importance as were stomatopods, crab megalops, and squids. It was concluded by Hotta and Ogawa (1955) that the tunas were nonselective in their feeding habits and ate whatever was available in the area.

Although these previous observations covered broad areas of the Pacific, no mention was made of any anchovy that may have been *S. buccaneeri* occurring in the stomach contents. An exception is a report by H. Nakamura (1936) on the food of yellowfin tuna caught in the Celebes Sea that mentioned an anchovy as one of the common food items. The area in which he found tunas containing the anchovy, the frequency of occurrence of the anchovy in tuna stomachs, and the numbers in which it occurred lead me to believe that it may have been *S. buccaneeri.*

METHODS

The stomachs of the troll and pole-and-line caught fish were removed after they were measured and sexed. Stomachs that appeared empty and those of most male tunas were examined in the field and their contents recorded. The rest were placed in muslin bags and preserved in 10% Formalin.[2] One of the objectives of the cruises was to collect 50 skipjack tuna and/or 50 yellowfin tuna blood samples from each school. Therefore, there were four occasions on which 50 stomach samples per school were collected.

In the laboratory, counts were made of the organisms in the stomachs whenever possible. Many of the partially digested fishes were identified by their vertebrae which were prepared by teasing away the muscles when necessary and staining with alizarin red. Skipjack tuna remains were identifiable by skeletons. Enough of the external characters of the anchovy usually remained for identification. Most of the other fishes were identifiable only to family. The stomach contents of the anchovy, which included many crustaceans, were identified by staining the organisms with methylene blue. Many of the copepods were identified to species but other invertebrates were identifiable only to major groups such as the Chaetognatha, Amphipoda, and shrimp.

STOMACH CONTENTS

EQUATORIAL EASTERN PACIFIC

The results of examining 268 skipjack tuna, 44 bigeye tuna (*Thunnus obesus*), 45 yellowfin tuna, 2 common dolphin, and 7 little dolphin (*Coryphaena equiselis*) caught on cruise 116 of the *Charles H. Gilbert* are presented in Table 1. The presence of *S. buccaneeri* in the stomach

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Frequency occurrence of organisms in the stomachs of 268 skipjack tuna, 44 bigeye tuna, 45 yellowfin tuna, and 9 dolphin (2 common and 7 little) examined from cruise 116 of the *Charles H. Gilbert.*

Food items	Predators							
	Skipjack tuna		Bigeye tuna		Yellowfin tuna		Dolphin	
	No.	%	*No.*	%	*No.*	%	*No.*	%
Fishes:								
Alepisauridae	2	0.7	--	--	--	--	--	--
Bramidae	3	1.1	1	2.3	1	2.2	--	--
Chaetodontidae	--	--	1	2.3	--	--	--	--
Diodontidae	1	0.4	--	--	--	--	--	--
Engraulidae:								
Stolephorus buccaneeri	35	13.1	20	45.4	--	--	--	--
Exocoetidae	3	1.1	--	--	1	2.2	3	33.3
Gempylidae	4	1.5	4	9.1	4	8.9	--	--
Nomeidae	--	--	1	2.3	1	2.2	--	--
Scombridae:								
Auxis rochei	1	0.4	--	--	--	--	--	--
Katsuwonus pelamis	5	1.9	--	--	--	--	--	--
Sternoptychidae	--	--	1	2.3	--	--	--	--
Zeidae	--	--	1	2.3	--	--	--	--
Unidentified	9	3.4	1	2.3	7	15.6	2	22.2
Chum	100	37.3	20	45.4	22	48.9	--	--
Crustacea:								
Amphipoda	2	0.7	--	--	2	4.4	--	--
Euphausiacea	1	0.4	--	--	--	--	--	--
Shrimp	2	0.7	1	2.3	--	--	--	--
Mollusca:								
Argonauta	6	2.2	--	--	1	2.2	--	--
Heteropoda	1	0.4	--	--	3	6.7	--	--
Squids	22	8.2	6	13.6	8	17.8	2	22.2
Chaetognatha	1	0.4	--	--	--	--	--	--
Stomach empty	136	50.7	15	34.1	17	37.8	5	55.6

contents of 13.1% of the skipjack tuna and 45.4% of the bigeye tuna examined was of particular interest. Of the invertebrates, squids were most frequently found in the contents. Many of the stomachs examined were empty.

This study revealed that only a few varieties of organisms were eaten in the oceanic environment, which contrasted markedly with Ronquillo's (1953) work showing a great diversity of organisms eaten in an environment influenced by land. The fact that *S. buccaneeri* was found only in the stomachs of tunas from two schools that were close to each other suggests that it was not widespread in this area.

SAMOA ISLANDS

Table 2 shows the results of examining 205 skipjack tuna, 23 kawakawa, 24 yellowfin tuna, and 1 common dolphin which were caught on cruise 117 of the *Charles H. Gilbert. S. buccaneeri* occurred very frequently in the stomachs examined. Other fishes occurring frequently belonged to the families Acanthuridae and Holocentridae. Stomatopod larvae, of the invertebrates, occurred most frequently in the contents. Many of the stomachs examined were empty.

The variety of organisms eaten around the Samoa Islands was limited. However, a comparison of the studies shows a greater diversity ingested around Samoa than in the equatorial eastern Pacific, probably because of the proximity to the islands. The distribution of *S. buccaneeri* was found to be widespread in this area. Their frequency of occurrence in the stomachs suggested that they were an important forage for the tunas and dolphins here.

TABLE 2.—Frequency occurrence of organisms in the stomachs of 205 skipjack tuna, 23 kawakawa, 24 yellowfin tuna and 1 common dolphin, examined from cruise 117 of the *Charles H. Gilbert.*

Food items	Predators							
	Skipjack tuna		Bigeye tuna		Yellowfin tuna		Common dolphin	
	No.	*%*	*No.*	*%*	*No.*	*%*	*No.*	*%*
Fishes:								
Acanthuridae	45	22.0	1	4.3	4	16.7	--	--
Balistidae	13	6.3	2	8.7	1	4.2	--	--
Bramidae	--	--	--	--	1	4.2	--	--
Carangidae	3	1.5	--	--	--	--	--	--
Chaetodontidae	11	5.4	--	--	1	4.2	--	--
Dactylopteridae	1	0.5	--	--	--	--	--	--
Engraulidae:								
Stolephorus buccaneeri	38	18.5	4	17.4	6	25.0	1	100
Exocoetidae	5	2.4	--	--	--	--	--	--
Gempylidae	13	6.3	--	--	--	--	--	--
Holocentridae	61	29.8	2	8.7	2	8.3	--	--
Molidae	1	0.5	--	--	--	--	--	--
Monacanthidae	3	1.5	1	4.3	--	--	1	100
Mullidae	2	1.0	--	--	--	--	--	--
Ostraciidae	1	0.5	--	--	--	--	--	--
Pomacentridae	--	--	--	--	1	4.2	--	--
Scombridae:								
Katsuwonus pelamis	19	9.3	--	--	--	--	--	--
Unidentified	8	3.9	--	--	--	--	--	--
Siganidae	8	3.9	--	--	--	--	--	--
Synodontidae (?)	6	2.9	--	--	--	--	--	--
Tetraodontidae	2	1.0	--	--	--	--	--	--
Chum	66	32.2	--	--	--	--	--	--
Unidentified	36	17.6	2	8.7	2	8.3	1	100
Crustacea:								
Amphipoda:								
Phronima sp.	--	--	--	--	1	4.2	--	--
Crab megalops	2	1.0	2	8.7	--	--	--	--
Phyllosoma larvae	1	0.5	--	--	--	--	--	--
Shrimp	--	--	1	4.3	--	--	--	--
Stomatopod larvae	7	3.4	3	13.0	1	4.2	--	--
Mollusca:								
Squids	20	9.8	--	--	1	4.2	--	--
Stomach empty	64	31.0	14	60.8	10	41.7	--	--

NOTES ON *STOLEPHORUS BUCCANEERI*

DISTRIBUTION

Strasburg (1960) described *S. buccaneeri* from Hawaii and proposed the common name, roundhead. His holotype was a specimen taken in a nearshore bait seine haul close to Lehua Island. He also found a few specimens in the stomach contents of kawakawa caught about a mile offshore from Oahu. Matsui (1963) found this species in the bait samples he obtained around the island of Maui.

The abundance of *S. buccaneeri* in Hawaiian waters is not known. This is largely because the Hawaiian skipjack tuna fishermen use the anchovy, *Stolephorus purpureus,* as their principal baitfish. These two fish are almost identical and therefore difficult to distinguish from one another. Anchovies regurgitated on deck and found in the stomach contents of tunas are assumed to be their baitfish. At times, however, Hawaiian skipjack tuna fishermen have reported seeing skipjack tuna feeding on what they refer to as "offshore nehu" (liberal translation of the Japanese term used), which more than likely is *S. buccaneeri.* The distribution of *S. purpureus* is inshore while that of the *S. buccaneeri* seems to be generally offshore. It is therefore proposed that another common name of *S. buccaneeri* might be offshore nehu.

Besides Hawaii, Whitehead (1967) gave the distribution of the *S. buccaneeri* as the Red Sea, Persian Gulf, Comoro Islands, east coast of Africa, Formosa, Hong Kong, Japan, the Philippines, Palau, southern India, and Singapore. He stated that they were very common in Hong Kong, Japan, and Hawaii.

Additional notes on the distribution of *S. buccaneeri* are given below; occurrences discussed are shown in Figure 1.

S. buccaneeri was first noticed on cruise 116 in the stomach contents of 4- to 12-kg bigeye tuna that were caught from a "boiling" school (see Scott, 1969) at lat 4°N and long 119°W. It was found again the next day in the stomach contents of skipjack tuna caught at lat 5°N on long 119°W, about 700 miles from Clipperton Island, the closest land. This occurrence is of interest because this species previously had been recorded only near land masses.

On cruise 117, *S. buccaneeri* was observed to be a common organism eaten by skipjack and yellowfin tunas, kawakawa, and dolphin caught around the Samoa Islands. Although it was very often eaten by tunas close to shore, it was neither seen nor caught while baiting in the inshore areas. Similarly, Robert E. K. D. Lee (pers. comm.) has found it eaten by yellowfin tuna and kawakawa caught near shore in the Fiji area but has not observed it during baiting operations in inshore waters.

In May of 1971 on cruise 53 of the *Townsend Cromwell, S. buccaneeri* juveniles were collected under a night light while the vessel was anchored in a depth of 25 m on Condor Reef in the Caroline Islands.

An estimated 20 kg of *S. buccaneeri* were caught in a close-to-surface haul made with a modified Cobb pelagic trawl (see Higgins, 1970 for a description of this trawl) 160 miles east of Agrihan Island in the Mariana Islands on cruise 55 of the *Cromwell* in November 1971. It was present in five other trawl hauls, in the stomach contents of a wahoo, *Acanthocybium solandri*, caught northwest of Ponape, and in several skipjack tuna caught by trolling north of Namorik during the same cruise.

John Naughton, National Marine Fisheries Service, Honolulu, informed me that several schools of yellowfin and skipjack tunas fished by the Hawaiian fishing vessel *Anela* around Majuro and Arno Atolls in ~~April~~ Feb. 1972 were feeding on schools of an anchovy resembling *S. buccaneeri*.

Wilson[3] cited that two Palauans trolling between Angaur and Peleliu Islands observed and sampled a school of kawakawa feeding on *S. buccaneeri*.

The occurrence of *S. buccaneeri* as discussed here in the equatorial eastern Pacific, Samoa Islands, Caroline Islands, Mariana Islands, Palau Islands, Marshall Islands, and Fiji in conjunction with previous records shows it to be a widespread Indo-Pacific (including eastern Pacific) species. Because it occurs in great abundance locally, such as at Fiji and the Samoa Islands, it is to be expected that details of its occurrence will be more likely noted.

SIZE

Most of the anchovies found in the stomach contents were in poor condition. The caudal fin and snout of many specimens were so badly digested that their standard lengths could only be estimated. The *S. buccaneeri* found in the bigeye tuna stomachs ranged from 30 to 57 mm in standard length (SL). Those found eaten by the skipjack tuna ranged from 20 to 58 mm. Those caught on cruise 117 of the *Charles H. Gilbert* near Samoa ranged from 23 to 78 mm. The samples from Condor Reef measured 15 to 30 mm while those from the trawl hauls caught close to the Mariana Islands ranged from 14 to 70 mm. The small postlarvae were semitransparent when alive and turned whitish when preserved in Formalin. They were identified by their exposed urohyal plate and posterior extent of their maxilla.

The presence of large numbers of postlarvae more than 100 miles from land, and adults as far as 700 miles from land, strongly suggests that this species is capable of completing its life cycle in an oceanic environment.

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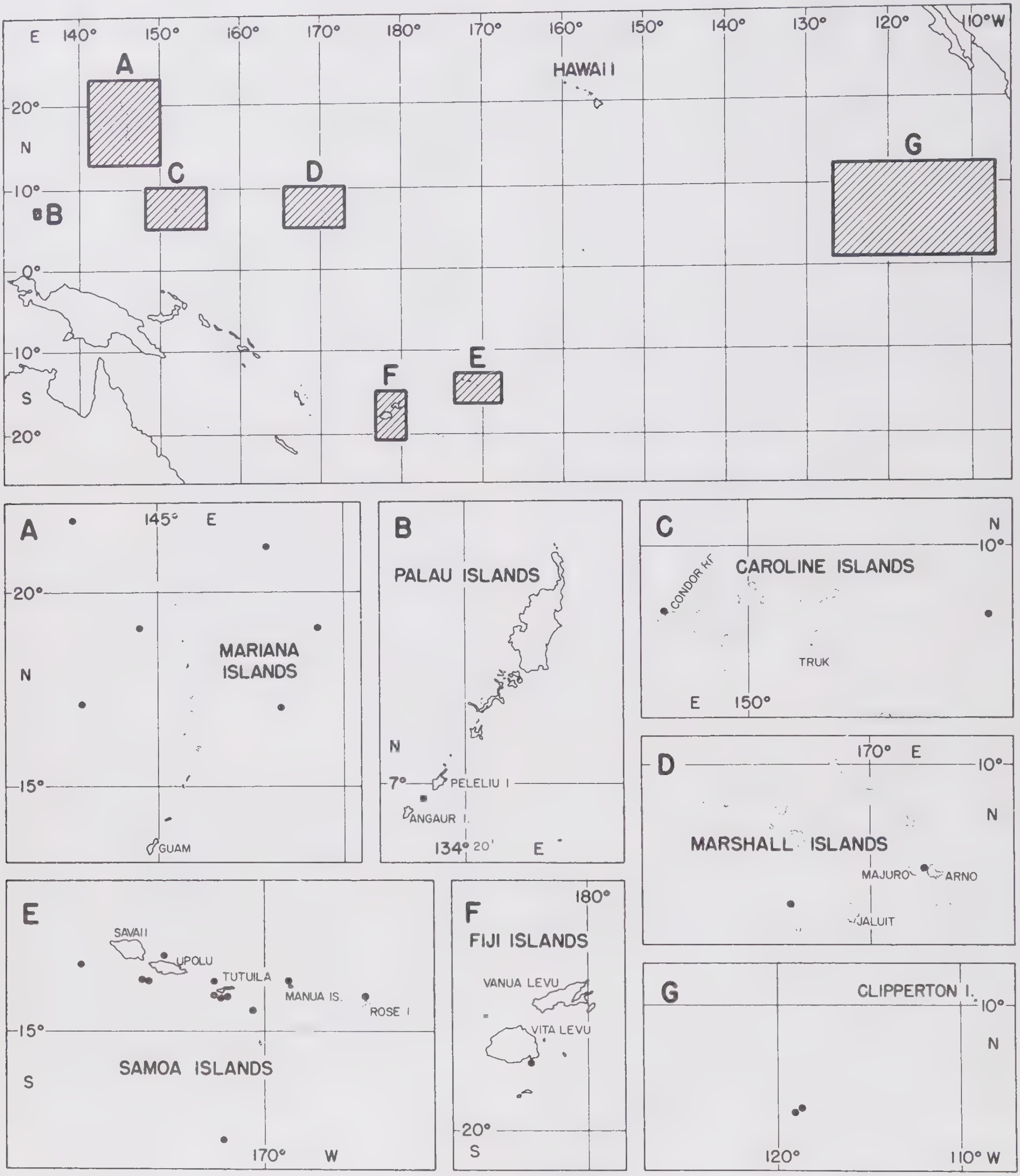
[3] Wilson, P. T. Observations of various tuna bait species and their habitats in the Palau Islands. Unpublished manuscript. Marine Resources Division, Trust Territory of the Pacific Islands, Saipan, Marianas 96950.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ANGAUR I.
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CONDOR RF
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ROSE I.
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FIJI ISLANDS
VANUA LEVU
VITA LEVU
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CLIPPERTON I.
10°
N
120°
110° W

FIGURE 1.—The distribution of *Stolephorus buccaneeri* in the Pacific covered in this study.

FECUNDITY

Ova of 32 specimens of *S. buccaneeri* obtained from tuna stomach contents were measured: Specimens were 38-55 mm SL. From each subsample, diameters of 30 or more of the ova from the most advanced mode were taken. Their distribution ranged from 0.4 to 0.8 mm and peaked at 0.5 mm. The ova were opaque, granulated, and classified as maturing.

Since there are no previous estimates of fecundity, ova from the most advanced mode from two *S. buccaneeri* ovaries were counted. This method was based on the assumption that all of the ova in this mode constituted a single spawning. A 44-mm specimen contained 595 ova in her left ovary and 830 in her right, a total of 1,398. A 39-mm individual had 340 ova in her left ovary and 454 in her right, a total of 794.

FOOD STUDY

The examination of 58 stomach contents of *S. buccaneeri* recovered from tuna stomachs showed that crustaceans were important in their diet, as shown in Table 3. Only one stomach was found empty. The stomachs of *S. buccaneeri* in this study contained primarily calanoid copepods and other organisms. The copepods that were abundant in one or more anchovy stomachs from the equatorial eastern Pacific were *Candacia truncata* and *Euchaeta marina.* The cyclopoid copepod, *Oncaea venusta,* was common in one stomach. Copepods found in abundance in one or more anchovy stomachs taken from tunas caught from the Samoa Islands were *Candacia bispinosa* (?) *C. catula, C. truncata, Centropages gracilis, Euchaeta marina* and *Temora discaudata. C. truncata* and *E. marina* were the only two species that were abundant in both areas. Not unexpectedly, the close-to-shore samples from Samoa were represented by more species than those of the oceanic equatorial eastern Pacific. It should be noted, however, that there were many copepodites and badly digested specimens in the equatorial eastern Pacific samples, while those from the Samoa Islands were larger and in much better condition for identification purposes. Hiatt (1951) examined the stomach contents of the nehu, *S. purpureus,* caught from five major baiting areas in Hawaii and concluded that nehu were selective feeders in that they took the crustacean elements in the plankton. He found important food items to be copepods, ghost shrimp (*Lucifer*), barnacle nauplii, shrimp larvae, and crab larvae.

ACKNOWLEDGMENTS

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TABLE 3.—The stomach contents of *Stolephorus buccaneeri* found in tuna stomachs in the equatorial eastern Pacific and the Samoa Islands (A = abundant, C = common, P = present). [The numbers examined are in parentheses.]

Food items	Samoa Islands			Equatorial eastern Pacific	
	Skipjack tuna (10)	Yellowfin tuna (6)	Kawakawa (4)	Bigeye tuna (23)	Skipjack tuna (15)
Copepoda:					
Calanoids:					
Candacia bispinosa (?)	A	--	--	--	--
Candacia catula	A	P	--	--	--
Candacia simplex	P	--	--	--	--
Candacia truncata	A	--	--	--	A
Candacia sp.	--	--	P	--	--
Centropages gracilis	A	--	--	--	--
Centropages sp.	--	--	P	--	--
Eucalanus sp.	--	--	P	--	--
Euchaeta concinna	P	--	--	--	--
Euchaeta marina	A	--	--	A	--
Euchaeta sp.	--	--	P	P	P
Lucicutia flavicornis	P	--	--	--	--
Nannocalanus minor (?)	--	P	--	--	--
Pleuromamma xiphias	P	--	--	--	--
Scolecithricella ctenopus	P	--	--	--	--
Scolecithrix danae (?)	C	--	--	--	--
Temora discaudata	A	P	--	--	--
Temora sp.	--	--	P	--	--
Undinula darwini	P	--	--	--	--
Unidentified calanoids	P	P	P	C	A
Cyclopoids:					
Copilia mirabilis	P	--	--	--	--
Copilia sp.	--	--	P	--	--
Corycaeus limbatus (?)	--	P	--	--	--
Corycaeus spesiosus	P	--	--	P	--
Corycaeus vitreus (?)	P	--	--	--	--
Corycaeus sp.	P	P	--	P	P
Farranula concinna (?)	P	--	--	--	--
Farranula gibbula (?)	P	P	--	--	--
Farranula sp.	--	P	P	P	--
Microsetella rosea	P	P	--	--	--
Microsetella norvegica (?)	--	P	--	--	--
Oncaea conifera	--	--	--	P	--
Oncaea venusta	--	--	--	C	--
Oncaea sp.	P	P	--	P	P
Sapphirina gastrica (?)	P	--	--	--	--
Sapphirina sp.	P	--	P	P	--
Unidentified cyclopoids	--	P	P	A	C
Amphipoda	P	--	--	--	--
Mysidacea	--	--	--	P	--
Shrimp juvenile	C	P	P	P	P
Crab megalops	--	--	P	--	--
Chaetognatha	A	P	P	P	P
Gastropod larvae	P	P	--	--	--
Heteropoda:					
Atlanta inclinata	P	--	--	--	--
Atlanta sp.	P	--	--	--	--
Bivalve larvae	--	P	--	--	--
Ostracoda	P	P	--	--	--
Polychaeta	P	--	--	--	--
Pteropoda:					
Creseis virgula	--	--	--	--	P
Unidentified fish	P	--	P	--	--

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Diel feeding migrations in tropical reef fishes

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KURZFASSUNG: **Tägliche Futtersuchwanderungen bei tropischen Riffischen.** Während der Dämmerungszeiten wandern viele tropische Fische zwischen ihren Ruheplätzen auf dem Riff und ihren Futterplätzen. Diese Wanderungen, die sowohl von tag- als auch von nachtaktiven Fischen durchgeführt werden, sind bedingt durch den Licht-Dunkel-Wechsel, und für viele Arten können sogar Zeit und Weg der Wanderung vorhergesagt werden. Das Muster der tagesrhythmischen Wanderungsbewegungen wird vor allem durch das Ausmaß von Bedrohungen durch Raubfeinde beeinflußt. Bewegungen in ungeschützte Gebiete, die vom Riff wegführen, sind am Tage nicht vorteilhaft. Bei Einbruch der Dunkelheit sind diese offenen Gebiete hingegen ein Konzentrationspunkt der Wanderungen aus dem Riff, wobei sich auch der Zusammenhalt der Fischschwärme verringert. Da Schwarmverhalten und Schutzsuchen die beiden wichtigsten Verteidigungseinrichtungen gegenüber Räubern darstellen, bedeutet das Aufgeben dieser Verhaltensweisen zu Beginn der Dämmerung, daß während der Nacht kleinere Riffische weniger bedroht sind als während des Tages. Für wandernde Schwarmfische dürfte eine geringe Variabilität der Verhaltensweisen von adaptiver Bedeutung sein. Nur durch ein koordiniertes Schwarmverhalten ist es offensichtlich möglich, innerhalb bestimmter Grenzen auf die verschieden optischen Marken, welche die Wanderwege kennzeichnen, zu reagieren. Vermutlich spielen die topographischen Gegebenheiten unter Wasser eine entscheidende Rolle für die Orientierung der Riffische.

INTRODUCTION

Diel feeding migrations are widespread among fishes on tropical reefs. Mostly, they are movements between resting locations and feeding grounds. Distances traveled by the different species vary widely, from at least several kilometers to just a few meters; the shorter movements would not be considered migrations except that they are basically the same phenomenon as the more extensive movements. These migrations occur mostly during twilight, as part of a general changeover between the day and night situations. Earlier, I described the twilight transition process in Kona, Hawaii (Hobson 1972), and contrasted the day and night situations in the Gulf of California (Hobson 1965, 1968); in each of these reports the significance of diel feeding migrations was stressed.

The migrations reflect the differing needs of the fishes during the two major segments of the diel cycle. Most fishes living on tropical reefs are active either by day or by night, with the diurnal species mostly inactive in darkness, and the nocturnal species mostly inactive in daylight (Hobson 1965, 1968, Starck & Davis 1966). When these fishes are inactive, their behavior relates primarily to their own security;

when they are active, their actions are dominated by their own feeding (Hobson 1972).

Tropical reef fishes obtain security when inactive in one of two ways: they school or they seek cover (Hobson 1968). The advantages of schooling have been discussed (Manteifel & Radakov 1961, Eibl-Eibesfeldt 1962, Hobson 1968); the advantage of seeking cover is obvious. At least many fishes return to the same schooling or sheltering sites for each period of inactivity (Hobson 1968, 1972). On the other hand, each of the wide variety of fishes on tropical reefs is active in a location that is related to its own specific feeding habits, and which may or may not be near its specific shelter site. Consequently, during the twilight transition period these fishes migrate between feeding grounds and resting locations.

This report is a synthesis of observations made between 1957 and 1972 during a continuous series of research projects at different locations in the Pacific Ocean (Gulf of California, Galapagos Islands, Hawaii and Micronesia). In all these studies, diving equipment was used to observe the fishes in their natural habitats.

CATEGORIES OF DIEL FEEDING MIGRATIONS

For convenience, the diel feeding migrations can be grouped into three broad, overlapping categories: (1) vertical migrations, (2) intra-reef migrations, and (3) migrations away from the reef. In all, the fishes travel in schools. There is no sharp distinction between these categories, and the activity of many species comprises elements of more than one type; nevertheless, each is characterized separately in the following.

Vertical migrations

This category includes the many small plankton feeders that move between feeding grounds in the water column, and shelter locations on the reef directly below. Examples include species of *Chromis* (Pomacentridae) and *Paranthias* (Serranidae), which are diurnal; and also species of *Myripristis* (Holocentridae) and *Apogon* (Apogonidae), which are nocturnal. All these plankton feeders are either diurnal or nocturnal. Without overlap, those feeding in daylight are inactive after dark, and those feeding at night are inactive in daylight (Hobson 1965, 1968, 1972, Starck & Davis 1966). Obviously, conditions of plankton feeding differ between day and night. Emery (1968) described the composition of plankton over Florida reefs as different between day and night. These vertical migrations were discussed earlier (Hobson 1968, 1972), and it was pointed out that one can predict when a given species will rise into the water column or descend to cover.

Intra-reef migrations

Many fishes travel each day between resting spots and feeding grounds that are widely separated on the reef. The timing and routes followed by many species are predictable. Among the more prominent of these are certain herbivores, including certain species of *Scarus* (Scaridae) and *Zebrasoma* (Acanthuridae) (Hobson 1972). These, like all herbivorous fishes on tropical reefs, are diurnal (Hobson 1965, 1968, Starck & Davis 1966). The diel feeding migrations of some plankton feeders include extensive lateral excursions across the reef, in addition to the vertical elements described above; included here are certain species of *Naso* (Acanthuridae), which are diurnal, and also certain species of *Myripristis*, which are nocturnal. These intra-reef migrations were discussed earlier (Hobson 1972).

Migrations away from the reef

The most extensive feeding migrations are performed by the many fishes that pass their inactive hours on the reef and go elsewhere to feed. Off-reef foraging by reef-based fishes is strictly a nocturnal phenomenon. During the day, most fishes in this category school in relatively inactive assemblages on or near the reef. They include certain species of *Harengula* (Clupeidae), *Pranesus* (Atherinidae), *Lutjanus* (Lutjanidae), *Haemulon* (Pomadasydae), *Selar* (Carangidae), *Sciaena* (Sciaenidae) and *Mulloidichthys* (Mullidae). Not all fishes in these groups migrate; many disperse at nightfall right at the schooling site, and forage throughout the night in the immediate area on the reef. Nevertheless, the major feeding grounds for diurnally schooling, nocturnally active fishes lie away from the reef. In the Gulf of California, expanses of open sand that lie adjacent to certain reefs are centers of activity for fishes that migrate at nightfall from schooling locations on the reef. However, during the day these same sand flats are accurately described as deserts because so little life is readily seen there (Hobson 1968).

For at least some of these diurnally schooling, nocturnally active fishes, both the timing and route of their off-reef migrations are predictable. In the Gulf of California I was able to predict to within a few minutes in the evening when *Harengula thrissina* (Clupeidae) would migrate away from its daytime schooling site to feeding grounds offshore. Furthermore, it became possible to chart the route this fish took during its migration (Hobson 1968). We were able to do the same with *Pranesus pinguis* (Atherinidae) at Majuro Atoll in the Marshall Islands (Hobson & Chess, in preparation).

The maximum distances traveled during these off-reef migrations vary, and for most species have not been determined. In the tropical western Atlantic Ocean, *Haemulon carbonarium* (Pomadasyidae) does not migrate, but instead confines its nocturnal foraging to the immediate vicinity of its diurnal schooling site; on the other hand, a congener, *H. flavoliniatum*, ranges at night up to 1.6 km from where it schools in daylight (Starck & Davis 1966). As an example from another family of fishes, *Pranesus pinguis* ranges up to 1.2 km from its diurnal schooling sites when it forages after dark in the lagoon at Majuro Atoll (Hobson & Chess, in preparation). Swimming underwater in the Gulf of California, I attempted to follow migrating schools of *Harengula thrissina* as they moved offshore in the evening; however, I always lost contact with them in the growing darkness before traveling more than about 400-500 m, at which point they had not changed course nor behavior.

The diurnally schooling, nocturnally active fishes, like all nocturnal reef fishes, are predators (Hobson 1965, 1968). Some that forage away from the reef, for example certain pomadasyids and sciaenids, seek benthic prey. Many others, however, including certain clupeids and atherinids, hunt free-swimming prey, much of it from the plankton. The vast majority of these prey-organisms are invertebrates, mostly crustaceans – relatively few fishes are taken (Hobson 1968). Many invertebrate animals, especially small, motile crustaceans, are more abundant in exposed positions at night than during the day (Longley 1927, Hobson 1965, 1968, Starck & Davis 1966). Earlier I stressed the importance of the relative availability of nocturnal invertebrates in determining activity patterns in tropical reef fishes (Hobson 1968).

FACTORS THAT INFLUENCE THE DIEL FEEDING MIGRATIONS

The influence of predators

The daily activities of tropical reef fishes show the overriding influence of two primary concerns: to eat and to avoid being eaten. Even though their own feeding is the primary concern of these fishes during their active periods, their actions, including the pattern of their feeding migrations, can be interpreted as strongly influenced by predators. Schooling and cover-seeking, the means whereby reef fishes attain security during their inactive periods, are also much in evidence during their active periods.

Aggregations in the water column

The small plankton feeders that forage in the water column characteristically remain in aggregations as long as they are away from the sheltering substrate, and aggregations are judged to provide the same protection as schools – if one wishes to distinguish between these assemblages (Hobson 1968). Furthermore, the distance they move above the reef can be interpreted as strongly influenced by the relative danger from predators. Thus, smaller individuals, which are more vulnerable to predators, do not feed as high in the water column as larger individuals, and when visibility is reduced both large and small remain closer to the reef than otherwise (Hobson 1972). Fish in these aggregations draw themselves close together when threatened; if the danger intensifies they may then dive to the sheltering rocks below. Thus both schooling and the need for proximate cover, as related to their security, influence the feeding activity and related movements of these fishes.

At night the situation is somewhat different. When nocturnal plankton feeders rise above the reef they too aggregate under moonlight, but increasingly disperse on darker nights (Hobson 1965, 1968). Some authors, for example Morrow (1948), have suggested that schools disperse at night because schooling fishes are no longer able to maintain visual contact. However, at least some fishes that have dispersed with darkness readily regroup if threatened, thus demonstrating that they are able to school under these conditions if necessary. For example, fishes scattered throughout darkened aquaria immediately formed a tight school when STEVEN (1959) and also THINES & VANDENBUSSCHE (1966) introduced an "alarm substance". Clearly, if aggregations are adaptive to such fishes because predation is reduced, then it would seem that the threat from predators diminishes with darkness. Other aspects of the feeding movements of reef fishes lead to this same conclusion, as illustrated below.

Reluctance to leave the reef during daylight

During the day, lateral excursions among reef fishes in Hawaii are essentially limited to the intra-reef movements of various herbivores and plankton feeders, especially various scarids, acanthurids and pomacentrids (HOBSON 1972). Adjacent expanses of open sea floor, like the sand flats that surround many reefs in the Gulf of California, are little visited by reef fishes in daylight. No doubt this in part reflects the relative absence of suitable food in these open areas during the day. Certainly, most herbivores have no reason to range over the open sandy areas, as the vegetation on which they graze is mostly attached to the hard substrates of the reef. However, even in areas where beds of sea grasses lie adjacent to the reefs, as in the tropical Atlantic Ocean, diurnal herbivores, mostly scarids and acanthurids, limit their off-reef grazing to the periphery of the beds, and thus never range far from the sheltering reef. Their grazing is so intense within this zone that the grasses are effectively cleared away within about 10 m of the reef. In describing this phenomenon, RANDALL (1965) speculated that these herbivores are kept close to the reef by the threat from predators. A similar situation exists with certain reef fishes that are adapted to feed in the sand, such as certain goatfishes (Mullidae). When sand flats lie adjacent to the reefs, as in the Gulf of California, such fishes frequently range along the periphery of these flats in daylight; however, they stay within retreating distance of the reef during this activity so that shelter is close-by if needed.

Nor can a lack of suitable food fully account for the fact that reef plankton feeders do not range into adjacent open regions during daylight. In the Gulf of California plankton is abundant in the water column above the sand flats surrounding many reefs, and a number of diurnal plankton-feeding fishes are adapted to feeding there. But these are not reef fishes; instead, they are specialized to an existence over the open sand, and all share an ability to find shelter in the only cover available, the sand itself. Thus the eel *Taenioconger* sp. (Congridae) keeps its tail in its burrow while extending its head as much as 40 cm up into the water column to pick plankton; when threatened, the eel quickly withdraws into its burrow. The wrasse *Hemipteronotus mundiceps* (Labridae) is more like the typical reef plankton feeders in that it aggregates up in the water column while feeding on plankton; however, whereas the reef plankton feeders dive to shelter among rocks or coral when seriously threatened, *H. mundiceps* possesses morphological specializations that allow it to dive headlong into the sand (HOBSON 1968). Clearly, in order to feed on plankton in the water column above these exposed, off-reef areas during the day a fish must be able to find effective shelter there when threatened.

The predators that threaten reef fishes

One need not look far to find the predators that so strongly influence the movements of reef fishes. Large carangids and other sizable fish-eaters patrol the inshore waters during the day, and are prominent on most tropical reefs. Nevertheless, in staying close to shelter or in schools the smaller fishes seem relatively secure from these predators during most of the day, even though the predators readily attack when an opportunity presents itself (Hobson 1968). Sometimes large carangids circle slowly about schooling areas in the Gulf of California for hours during the day without making an aggressive move, then instantly attack when some segment of the school has become disorganized, or some individuals isolated (Hobson 1968). Just as schooling fishes tighten up their schools when predators threaten, other reef fishes react to approaching predators by moving closer among reef irregularities, which preclude the space-demanding maneuvers of many large predators. The threat from predators, therefore, is a major reason why open areas are generally avoided by reef fishes in daylight.

Crepuscular period of increased vulnerability

The large piscivores on the reefs hunt most effectively during twilight (Hobson 1965, 1968, Starck & Davis 1966). However, the migrating fishes – both diurnal and nocturnal – are in their shelter sites when the predators are most active. The diurnal herbivores that had migrated to graze elsewhere on the reef have already returned to their nocturnal resting places, and the diurnal plankton feeders have descended to the reef for the night. Furthermore, the nocturnal plankton feeders have not yet ascended into the water column. Thus there is at this time an interim in the twilight transition activities. The same phenomenon occurs during morning twilight, when the sequence of events is reversed. Earlier, I described these evening and morning interim periods in Hawaii, and their relation to the activity of predators (Hobson 1972). The diurnally schooling, nocturnally active fishes, still in their daytime locations and unable to take physical shelter on the reef, are increasingly attacked by the large predators at this time (Hobson 1968). After peaking, the predation ceases, and the predators withdraw. Most of the schooling prey, which are nocturnal predators, then migrate to their off-reef feeding grounds (Hobson 1968). This occurs with the approach of last light, suggesting that the mode of attack used by many large piscivores loses its effectiveness when available light falls below a certain level.

Decreased threat from predators at night

Thus, with nightfall many schooling fishes stream out into the open regions around the reef. Those migrating some distance away remain in a compact school en route, but once on the grounds become increasingly dispersed. Though variably dispersed, the schools of some, for example *Microlepidotus inornatus* (Pomadasyidae) in the Gulf of California (Hobson 1968), continue to operate as a unit during the night. Others are active as solitary individuals, or in small groups. For example, the atherinid *Pranesus pinguis* swims in a school as it migrates offshore at nightfall in the lagoon of Majuro Atoll; however, during the night, while feeding on plankton at the water's surface, it is widely scattered, with 2–4 m between each individual (Hobson & Chess, in preparation).

Thus, the two suggested mechanisms whereby smaller fishes attain a measure of security against predators during the day – schooling and staying close to shelter – become less evident after dark. Not only do small fishes swim freely into exposed regions at night, but, should the need arise, generally they are incapable of taking shelter in the sand. As already stated, this capability seems a requirement of fishes active in these regions during the day. All of this is further evidence that small reef fishes face less of a threat from predators at night than they do during the day.

The schooling fishes that migrate away from the reef at night, like the nocturnal plankton feeders over the reef, described above, are increasingly dispersed on darker nights. Moonlight exerts a strong influence on fishes. Randall & Brock (1960), among others, suggested that various predominantly diurnal piscivores feed at night when there is a bright moon. The tendency of small fishes to stay closer together under moonlight is probably adaptive for this reason. Certainly, an experienced human is able to operate effectively in clear tropical water at night with no more illumination than moonlight. As moonlight diminishes, so apparently does the danger from fish-eating predators.

Some piscivores are adapted to hunt smaller fishes at night. The eastern-Pacific Ocean *Caranx marginatus* (Carangidae), which may grow to over 600 mm long, feeds nocturnally (Hobson 1968), and larger individuals of this species are mostly piscivorous. Similarly, *Selar crumenophthalmus* and *Selene brevoorti*, two other carangids, prey on clupeids at night in the Gulf of California (Hobson 1968). These predators are all large-eyed, indicating that they hunt visually after dark, just as most diurnal piscivores do in daylight. Nevertheless, compared to the number of large fish-eating predators abroad in daylight, few seem to be active at night.

Although the behavior of smaller fishes after dark can be interpreted as indicating a diminished threat from piscivores, it is possible that a different sort of predator is afield after dark, one against which schooling or proximate cover offer no protection. Manteifel & Radakov (1961) stated that nocturnal predators do not use vision, but rather rely on olfaction and lateral-line receptors to locate their prey, finally concluding that the school has no protective value at night. However, I know of no such predator that significantly threatens free-swimming tropical reef fishes. Earlier (Hobson 1966, 1968) I discussed visual cues in the sea that could provide targets for visually orienting nocturnal predators.

Importance of activity in numbers

It is a characteristic of the feeding migrations that the fishes move in schools. Even species that are largely solitary when their activity is confined to a limited area will join with others of their kind when migrating. Probably the advantages of the school under this circumstance involves some form of social facilitation. One would expect each individual in a school to be differentially receptive to a given cue, but that member interactions would tend to synchronize the overall response to make actions of the unit more consistent. Thus through group actions fishes are better able to respond with precision to the various cues that regulate their activity. Behavior among fish in a group is less variable than it is among the same number of fish acting independently. Welty (1934) considered this in his concept of "group cohesion", and it is a well-known charcteristic of fish schools. However, reports on the adaptive significance of schooling have neglected this phenomenon.

The diverse manner in which fishes congregate (e. g. Breder 1967) suggests that multiple functions are served – probably more than one simultaneously. The role of fish groups in reducing predation has been extensively dealt with above. Reducing variable behavior seems to be another important function, especially when precise timing or a particular type of response is required in a given stimulus situation. This phenomenon appears especially adaptive to migrating fishes, whose responses to the various cues marking their migration routes may be refined to within acceptable limits by group action. Consider the many species that forage away from the reef during the night. It may be that only through coordinated group action can such fishes navigate in relatively featureless surroundings offshore, and still consistently find their way back to their specific schooling sites at the proper time in the morning.

Importance of submarine landmarks

Diurnally schooling fishes that swim away from the reef at night tend to return to the same locations each morning, with the daytime schooling sites often located close to prominent topographical features. For example, during observations over six years in the Gulf of California, *Haemulon sexfasciatum* (Pomadasyidae), which ranged widely when foraging at night, schooled each day close to a particular large rock (Hobson 1968). Certainly a chaotic situation would exist if the many different schools coexisting in a given region, and ranging far afield at night, did not consistently assemble in specific locations when they returned to the reef in the morning. This close association of reef fishes to particular topographical features is not confined to species that migrate. Residency in well-defined locations is characteristic of most reef fishes, as indicated by the tagging efforts of Bardach (1958), Springer & McErlean (1962), Randall (1961) and others. Probably this involves a mechanism whereby spatial organization is maintained among fishes on the reef. Williams (1957) and others have suggested that reef fishes determine their position under certain circumstances by orienting on topographical features.

SUMMARY

1. Many tropical reef fishes that feed during the day rest at night, whereas many that feed at night rest during the day. The feeding grounds of many are some

distance from their resting grounds. Thus they migrate between these two locations during twilight as part of a general changeover between diurnal and nocturnal situations.

2. At least many of these migrations are predictable, both as to time and to the route taken. The distances traveled vary between species, ranging from just a few meters, to more than several kilometers.
3. The pattern of migrations is strongly influenced by the relative threat from predators at different periods of the diel cycle.
4. During the day, migrations of reef fishes are limited to intra-reef movements: short vertical movements by certain plankton feeders, and lateral excursions from one part of the reef to another by certain herbivores and plankton feeders. Movements into the open regions that lie adjacent to many reefs are not adaptive in daylight due largely to a danger from predators.
5. Despite constant threat from predators during the day, smaller reef fishes remain relatively secure during most of this period by staying close to shelter, or by schooling. However, these defenses are less effective during twilight, when the danger from predators intensifies. The diurnal migrators return to the shelter of their resting places prior to that part of evening twilight when danger is greatest, and the nocturnal migrators usually do not expose themselves for their nightly foraging until after the period of maximum danger has passed. During morning twilight the sequence is reversed.
6. The major mechanisms whereby smaller reef fishes reduce predation during the day – schooling and staying close to shelter – are less evident at night. Not only do reef fishes range freely at night into the open regions that are avoided in daylight, but their schools are more loosely defined, and many are active as solitary individuals or in small groups. The tendency for looser associations and ranging farther afield increases on darker nights.
7. Most predators that threaten reef fishes are visual feeders whose mode of attack loses effectiveness when light falls below a certain level. Although they operate to some extent under moonlight, they threaten small reef fishes less at night than during the day.
8. In addition to whatever other ways a school may be adaptive, by reducing variable behavior among its members the school is especially important to migrating species. Responses to the various cues that mark the migration routes may be refined to within acceptable limits for the population as a whole only by coordinated group action.
9. Submarine topographical features are important reference points for migrating reef fishes.

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FEEDING ORIENTED MOVEMENTS OF THE ATHERINID FISH *PRANESUS PINGUIS* AT MAJURO ATOLL, MARSHALL ISLANDS

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ABSTRACT

The feeding behavior of the atherinid *Pranesus pinguis* was studied in the lagoon at Majuro Atoll, Marshall Islands, during March 1972.

During the day, individuals larger than about 35 mm (standard length) assemble in relatively inactive schools along the shore. Shortly after sunset the schools migrate offshore to feeding grounds in the lagoon, following the same route night after night. Once out in the lagoon the schools disperse, and individuals 2 to 4 m apart feed on plankton at the water's surface throughout the night. Their prey include hyperiid amphipods, caridean shrimp larvae, myodocopid ostracods, the tretomphalus stage of foraminiferans, and calanoid copepods. Most of their prey are at the surface at night. but at greater depths in daylight. At first morning light the silverside begin to concentrate in the shoreward part of their feeding ground. Then about 45 min before sunrise, having reached daytime proportions, the school moves inshore over the same route it had taken outward the night before and at about 20 min before sunrise arrives at its diurnal schooling site to take up its relatively inactive daytime mode.

In contrast, limited evidence indicates that individuals smaller than about 30-mm standard length feed by day but not at night.

The silverside *Pranesus pinguis* (Lacépède) is widespread in the western Pacific and Indian Oceans (Schultz, 1953) and is a potential baitfish for tuna fishermen (Hida, 1971). Because biological information of the species does not exist, we studied its feeding activity in the lagoon at Majuro Atoll, in the southeastern Marshall Islands, from 16 to 25 March 1972.

Majuro Atoll is a ring of shallow coral reefs and low islands encircling a lagoon about 40 km east to west and 10 km north to south (Figure 1). Around the perimeter of the lagoon a narrow shelf of sand and isolated coral heads extend offshore under 1 to 6 m of water. At the outer edge of this shelf, several hundred meters from shore, the sea floor falls abruptly to a depth of 40 m, which is the approximate water depth over most of the lagoon.

The study was centered on silverside that schooled during the day (Figure 2) along the shore of Arniel Island (Figure 3). The behavior of fish in this school was judged typical of that seen in other members of the species during a limited survey along the shores of other islands bordering the lagoon.

Movements and other behavior of this fish were observed directly using a face plate and snorkel at all hours of day and night over the 10 days we spent at Majuro. Specimens were collected for analysis of gut contents, and plankton samples were taken in the lagoon during both day and night. Sampling methods and procedures are described below where pertinent. All lengths given for the silverside are standard length. Because the horizon frequently was obscured by clouds, times of sunrise and sunset were calculated using the Nautical Almanac, U.S. Naval Observatory.

ACTIVITY PATTERN

The Diurnal School

During each day, individuals about 35 to 65 mm long hovered in a quiet school that was strung out along the shore. Here, where it is 1 to 2 m deep, the school occupied most of the water

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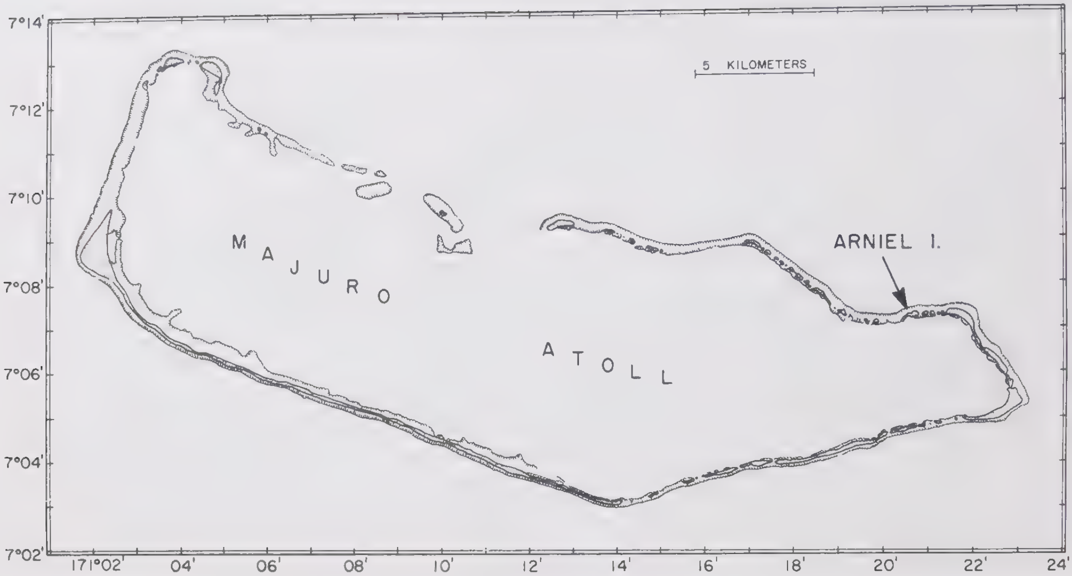
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FIGURE 1.—Majuro Atoll, Marshall Islands, showing Arniel Island. Adapted from U.S. Hydrographic Office chart 6087.

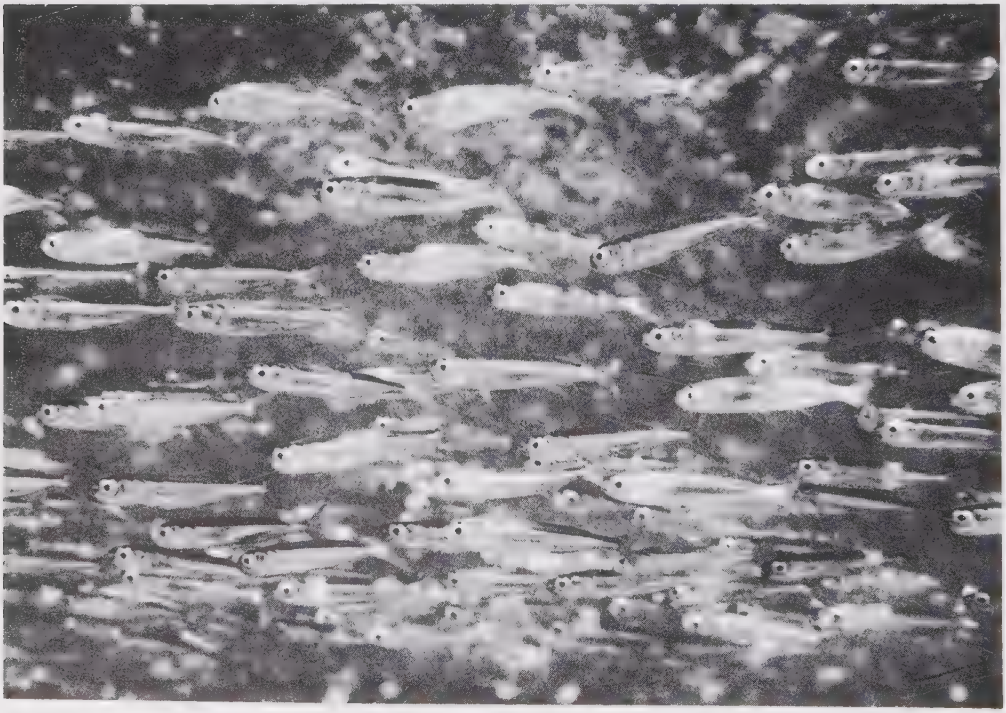

FIGURE 2.—*Pranesus pinguis* schooling during the day along the lagoon beach of Arniel Island.

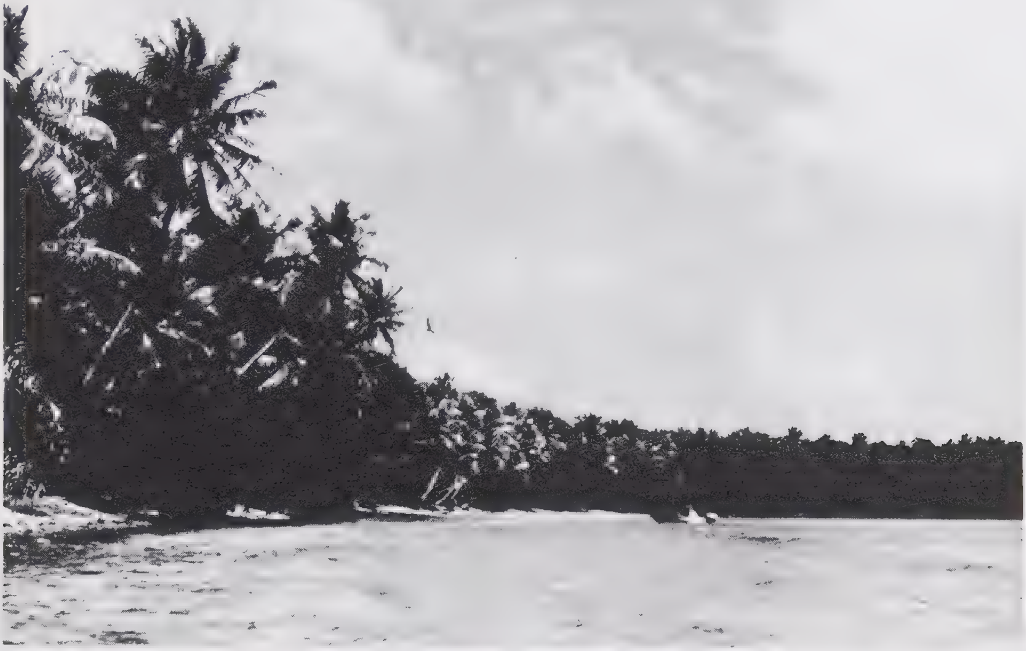

FIGURE 3.—The lagoon shore of Arniel Island, viewed from the point at the western end of the bay in which this study was centered.

column. Perhaps the outstanding characteristic of the school at this time was the inactivity of its members.

The situation began to change late in the afternoon, when fish in the school gradually drew together at a point in the center of the bay. By sunset the school was a compact unit, concentrated just beneath the surface of the water.

As evening approached, the fish became increasingly restless, and often the school was briefly in motion, only to return to its original position. The fish were highly responsive to disturbances at this time. Repeatedly a segment of the school exploded from a point within, so that a void suddenly appeared. Sometimes this maneuver could be traced to a predator—usually a carangid or a belonid—but more often no basis for the action was noted.

The Offshore Migration

Shortly after sunset the silverside migrated away from their daytime schooling site. We recorded this phenomenon on all three occasions when observations were made at this time of day.

The school could not be seen effectively from out of water at this time of day, owing to the fading light and wind-waves on the water's surface. Consequently, we watched from underwater: once (21 March) from the center of the school, when the fish around us began to migrate 14 min after sunset; once (22 March) at the eastern edge of the school, when the fish in view began moving out at 9 min after sunset; and once (24 March) at the western edge, when the observed fish got underway at 4 min after sunset. Because we made observations from three widely separated parts of the school, these times are not directly comparable. Nevertheless, on each occasion the last of the silverside had left the schooling site about 10 min after the first individuals moved out.

When the migration was recognized to be underway, one of us remained at the schooling site to follow developments there, while the other accompanied the migration. The major segment of the school did not move directly offshore; rather, each evening it headed westward along the beach. It continued in this direction until reaching the point of land at the western end of the bay (Figure 4) and then veered offshore over the deeper water of the lagoon, where contact with it was lost.

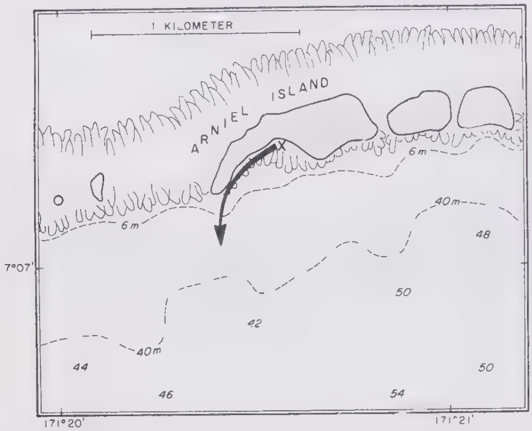

FIGURE 4.—Route taken by the silverside when migrating offshore from Arniel Island. The diurnal schooling site of this fish is marked by "X." Soundings are in meters. Adapted from U.S. Hydrographic Office chart 6087.

Nocturnal Activity

Later during the night the silverside were found offshore in the lagoon, spread out just below the surface of the water, with 2 to 4 m between each fish. They remained there throughout the night, feeding on plankton (discussed below); although some of them ranged as much as 2 km out into the lagoon, most occurred within 1 km of the beach. Their distribution at 0400 h on 24 March, more than 2 h and 30 min before sunrise, is illustrated in Figure 5. The method used to obtain the distribution of silversides in Figure 5 is as follows: Running a skiff along Arniel Island, we established a speed that took us the length of the Island in precisely 4 min. Maintaining this speed, we then headed out into the lagoon from the center of the bay, using a light on the opposite side of the atoll to stay on course. Upon passing over the dropoff into deeper water, we used a hand light to count the number of silversides in our path during each minute of a 10-min run. These fish are readily seen using this method owing to the characteristic reflections from their silvery bodies when struck by the light.

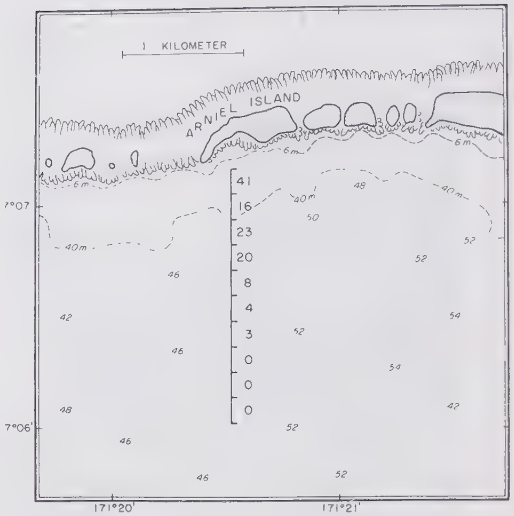

FIGURE 5.—Distribution of silverside at the surface along a transect running offshore from Arniel Island at 0400 h on 24 March 1972 (see text for method used). Adapted from U.S. Hydrographic Office chart 6087.

At first morning light, about 1 h and 15 min before sunrise, the silverside began to concentrate in the shoreward part of their feeding ground. Soon it was apparent that the silverside were regrouping directly offshore from where they had departed the island the previous evening.

The fish continued to regroup until about 30 min before sunrise, by which time the school had attained daytime proportions and was ready to return to its diurnal location.

The Inshore Migration

The lagoon was glassy-calm on each of the three consecutive mornings that we witnessed the inshore migration (23-25 March) so that observations could be made from above the surface of the water near the daytime schooling site. By noting agitation on the water's surface, the school was seen arriving each morning off the point at the western end of the bay, and then progressing steadily eastward along the shore. Thus, in the morning the silverside reversed the route they had taken offshore the night before. The vanguard of the school arrived at the diurnal schooling site on each of the three mornings at 20, 18, and 16 min before sunrise, respectively. Because these observations, unlike those of the evening, were made from the same vantage point, they are directly comparable.

For a while after arriving inshore, the silverside remained in a compact school but progressively strung themselves out along the beach until the midday situation prevailed.

P. pinguis is another example of a fish that assembles in relatively inactive schools in shallow water during the day and then migrates to feed elsewhere at night. This phenomenon is known in certain clupeids, pomadasyids, carangids, sciaenids, and lutjanids in the Gulf of California (Hobson, 1965, 1968), and has also been reported for many species in the tropical Atlantic (Starck and Davis, 1966). Obviously it is a widespread activity pattern among shore fishes in tropical seas.

FEEDING HABITS

The inactivity of silverside (>35 mm long) that hover in their inshore schools during the day indicates that they do not feed at this time. To obtain more data on this question, specimens were collected for gut-content analysis three times during the day (19 March). The first collection was made early in the day (0700 h); the second collection, during midday (1030 h); and the third collection, late in the day (1600 h). Ten specimens from each collection were examined.

All 10 specimens (61 to 73 mm long) examined from the early collection had material in their guts, which on the average were about 20% full. Composition of these gut contents, ranked as the mean percent (by volume) of each item in all silverside specimens, were as follows: hyperiid amphipods, 49.6%; caridean shrimp larvae, 6.7%; calanoid copepods, 6.2%; ostracods, 5.5%; crab megalops, 2.3%; mollusk veliger larvae, 1.0%; polychaetes, 0.5%; foraminiferans (tretomphalus stage), 0.4%; and unidentified, well-digested material 27.8%. Digestion had damaged all of this material so that identifications could be made only to major groups.

Of the 10 specimens (61 to 70 mm long) examined from the midday collection, three were empty; the guts of the remaining seven were on the average about 15% full, but digestion had reduced this material to a soup of unidentifiable fragments.

Finally, the guts of all 10 specimens (58 to 64 mm long) from the collection made late in the day were empty.

The data clearly demonstrate that the silverside in these inshore schools do not feed during the day. But even in those individuals taken during early morning, digestion had damaged the gut contents beyond the point where a precise analysis could be made. Being small themselves, the silverside take tiny prey, mostly under 2 mm long, whose identifying features do not resist digestion well.

To obtain material for a detailed analysis of food habits, we went 200 to 800 m offshore from Arniel Island between 0400 and 0500 h on 23 and 24 March. Here, using a dip net and flashlight from a moving skiff, we collected 64 specimens between 35 and 69 mm long, which were immediately placed into a 10% Formalin[2] solution. With this procedure, we obtained fish that were actively feeding, and whose gut contents (Table 1) included fresh material. In Table 1, the items are ranked by a "ranking index," which is computed by multiplying the mean percent (by volume) of each item in the gut contents of all silverside specimens by the ratio of silverside containing that item to total silverside sampled. Thus, for *Hyperia bengalensis* found in silverside collected on 23 March, the ranking index is 46.71 × 30/31 = 45.20. To increase the precision of the ranking index, the mean percent of each item in the gut contents is carried to two decimal places. The actual observed values for individual fish were estimated to the nearest percent, except where the estimate was <1.00, in which case the estimate was to > or <0.50%. For purpose of calculating the mean percent,

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[2] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Gut contents of 64 silversides collected on 23 and 24 March 1972.

Rank	Item	Size (mm)		Number of silverside with this item	Mean percent (vol.) of each item in all silverside specimens	Ranking index
		Mean	Range			
	Gut contents of 31 silversides 35 to 67 mm long, collected on 23 March 1972					
1	*Hyperia bengalensis* (hyperiid amphipod)	1.6	(1.0-2.0)	30	46.71	45.20
2	Tretomphalus stage of foraminiferan(s)	0.3	(0.2-0.7)	14	18.43	8.32
3	Caridean shrimp larvae	1.7	(0.5-6.0)	18	7.84	4.55
4	Myodocopid ostracods	1.3	(0.5-2.0)	18	6.61	3.83
5	*Undinula vulgaris* (calanoid copepod)	1.5	(1.0-2.0)	11	1.94	0.69
6	Crab megalops	2.0	(1.0-3.0)	4	3.70	0.48
7	*Lucifer* (sergestid shrimp)	7.0	(4.0-16.0)	3	4.03	0.39
8	*Candacia discaudata* (calanoid copepod)	1.6	(1.0-2.0)	8	1.19	0.31
9	Insects	3.0	(2.0-5.0)	3	1.77	0.17
10	Mysids	5.0		2	1.77	0.11
11	Veliger larvae (mollusks)	0.9	(0.5-1.5)	5	0.22	0.04
12	Zoea larvae (crabs)	1.5	(1.0-2.0)	2	0.32	0.02
13	"Other" calanoid copepods	1.0		2	0.13	0.008
14	Polychaetes	—		1	0.13	>0.004
15	*Saphirella* sp. (cyclopoid copepod)	0.9	(0.7-1.0)	2	0.06	<0.004
16	*Oncaea* sp. (cyclopoid copepod)	0.3		1	0.03	<0.001
17	Larvaceans	1.0		1	0.03	<0.001
	Also, unid. amorphous material	—		8	5.09	1.27
	Gut contents of 33 silversides 35 to 69 mm long, collected on 24 March 1972					
1	*Hyperia bengalensis* ((hyperiid amphipod)	1.9	(1.0-3.0)	24	28.28	20.57
2	Myodocopid ostracods	1.5	(0.5-2.0)	21	14.75	9.39
3	Tretomphalus stage of foraminiferan(s)	0.3	(0.1-0.8)	20	12.00	7.27
4	*Candacia discaudata* (calanoid copepod)	1.5	(0.5-2.0)	15	4.46	2.02
5	Caridean shrimp larvae	2.2	(1.0-4.0)	12	4.88	1.77
6	*Undinula vulgaris* (calanoid copepod)	1.6	(1.0-2.5)	12	2.73	0.99
7	Mysids	5.5	(2.0-7.0)	5	5.60	0.85
8	"Other" calanoid copepods	0.9	(0.8-1.0)	8	2.25	0.54
9	Insects	2.5	(1.5-3.0)	7	1.89	0.40
10	Veliger larvae (mollusks)	0.7	(0.3-1.0)	9	1.45	0.39
11	Polychaetes	—		4	0.88	0.11
12	*Labidocera acuta* (calanoid copepod)	2.0	(1.5-2.5)	3	0.64	0.06
13	*Lucifer* (sergestid shrimp)	3.0	(1.0-5.0)	2	0.60	0.04
14	Crab megalops	5.0		1	1.20	0.04
15	*Oncaea* sp. (cyclopoid copepod)	0.7	(0.5-1.0)	3	0.36	0.03
16	*Saphirella* sp. (cyclopoid copepod)	0.8	(0.5-1.0)	4	0.17	>0.02
17	Stomatopod larvae	5.0		1	0.60	<0.02
18	Alphaeid shrimp	4.0		1	0.30	0.009
19	Zoea larvae (crabs)	3.0		1	0.30	0.009
20	Gammarid amphipods	1.0		1	0.20	0.006
21	*Globigerina* sp. (foraminiferan)	1.0		1	0.03	<0.001
	Also, unid. amorphous material	—		10	12.57	3.81
	unid. crustacean fragments	—		5	3.86	0.59

>0.50 was considered to be 0.75, and <0.50 was considered to be 0.25.

A few forms predominated in the silverside diet when these observations were made. The hyperiid amphipod *Hyperia bengalensis* was especially important, with other major prey including: the tretomphalus stage of a foraminiferan(s); myodocopid ostracods; caridean shrimp larvae; and two calanoid copepods: *Candacia discaudata* and *Undinula vulgaris*. These forms constituted over 90% of the food in the guts of the silverside that were sampled.

PLANKTON AS PREY FOR THE SILVERSIDE

To determine whether these forms were selected by the silverside or were taken only in numbers relative to their abundance in the plankton, net hauls were made concurrently with the fish collections. The plankton sampled were from the lagoon between 22 and 24 March 1972. Additional plankton collections were made in the same location during daylight, thus providing a comparison of the plankton between day and night. These data (Table 2) demonstrate the importance of sampling the plankton right along with the fish. The methods of collecting were as follows: Seven tows were made over one 500-m course (duration approximately 15 min), about 600 m offshore from Arniel Island using a 1-m net with a 0.333-mm mesh. Night tows were made on 23 and 24 March at the same time that the fish were collected for gut-content analysis (Table 1). Day tows were made at 1600 h on 22 March and at 1200 h on 24 March. Six of the tows were paired: on both nights and during the day of 24 March one tow at 4 to 5 m deep was immediately followed by a second tow with the net breaking the water's surface. On the day of 22 March only the 4- to 5-m depth was sampled. The analysis is of 10% subsamples, one taken from each collection. Significantly, except for a lone alphaeid shrimp in one gut, every prey species found in the silverside occurred in the night plankton samples.

Clearly there was a great difference in the composition of the plankton between day and night, and a lesser though significant difference from one day or night to the next. Furthermore, these differences are reflected in the feeding habits of the silverside.

The daytime samples had greater volume (measurements by displacement: day volume—mean 16 ml, range 11-26 ml; night volume — mean 13 ml, range 10-15 ml), but this was due mostly to there being more chaetognaths in those collections. As shown in Table 2, there were many more species in the plankton samples taken at night, and most of the species present in both day and night collections were more numerous in the night collections. This is especially true of forms taken as prey by the silverside. Nevertheless, although many forms taken by silverside were relatively numerous, they contributed relatively little to the total volume of the plankton samples, even at night.

Major Prey Organisms

The habits of the silverside are better understood after a closer look at some of its major prey.

Hyperia bengalensis

This amphipod was the major prey of the silverside at the time of this study. Our collections indicate that it is present at the surface in greater numbers at night. This widespread species has been found elsewhere to move toward the surface after dark, and retreat to deeper water in daylight (G. J. Brusca, Humboldt State College, Calif., pers. comm.). It was equally numerous at the surface and at the 4- to 5-m depth in all night collections, but occurred in only 1 day collection, here in lesser numbers (Table 2).

Although *H. bengalensis* was the top-ranked prey on both nights, it was considerably more numerous in the gut samples on 23 March than on 24 March. Significantly, it was also more numerous in the plankton samples taken on the 23d (Table 2).

Tretomphalus Stage of Foraminiferans

Perhaps several species are represented here, but all are characterized by a calcareous, gas-filled float that buoys them at the surface (Myers, 1943). Undoubtedly, this habit accounts for this form's high incidence among prey of the surface-feeding silverside. One would not expect the tretomphalus to migrate vertically between day and night, and the data indicate they do not (Table 2).

Although the tretomphalus were well represented in the plankton collections on both nights, they were more numerous on 24 March; nevertheless, although their importance as prey on the two nights was similar, they were the third-ranked prey on the 24th and second-ranked prey on the 23d.

Myodocopid Ostracods

Being relatively numerous in the night plankton collections, but absent from the day plankton collections, these forms, like the hyperiid, apparently rise toward the surface in darkness, and descend to deeper water in daylight. Myodocopids were prominent among the gut contents on both nights, but whereas they ranked only fourth on the 23d, they ranked second on

TABLE 2.—Plankton samples 22, 23 and 24 March 1972.

Organism	Size (mm)	Number of individuals							Rank in silversides gut contents	
		Night				Day				
		Surface		4-5 m depth		Surface	4-5 m depth			
		23 Mar.	24 Mar.	23 Mar.	24 Mar.	24 Mar.	22 Mar.	24 Mar.	23 Mar.	24 Mar.
Foraminiferans										
Globigerinids	0.2- 1.0	130	130	68	160	48	5	147	—	21st
Tretomphalus	0.2- 0.6	18	58	0	2	10	12	2	2d	3d
"Other " forams	0.6- 2.0	18	6	0	41	2	1	8	—	—
Coelenterates										
Siphonophores	3.0-10.0	9	3	16	0	7	37	14	—	—
Flatworms										
Turbellarians	1.0	0	1	0	0	0	0	0	—	—
Annelids										
Polychaete larvae	0.5- 4.0	35	6	12	18	0	16	2	14th	11th
Polychaete post lurvae	4.0	3	0	0	0	0	0	0	—	—
Brachiopod larvae	0.5- 2.0	8	0	4	3	0	20	0	—	—
Mollusks										
Veligers	0.2- 0.5	36	47	25	70	15	84	40	11th	10th
Heteropods (1 sp.)	0.5- 3.0	12	2	6	1	1	21	8	—	—
Pteropods (2 sp.)	1.0- 8.0	6	6	3	5	1	17	0	—	—
Crustaceans										
Myodocopid ostracods	0.4- 2.0	50	150	160	190	0	0	0	4th	2d
"Other" ostracods	—	4	18	35	20	24	27	0	—	—
Cladocerans	0.5	0	1	0	0	0	0	0	—	—
Calanoid copepods										
Candacia discaudata	1.5- 3.0	19	370	16	330	0	0	0	8th	4th
Undinula vulgaris	1.0- 3.0	173	90	200	180	11	192	191	5th	6th
Labidocera acuta	1.0- 3.0	24	2	15	1	1	0	8	—	12th
"Other" calanoids	0.5- 2.0	54	1,304	90	390	34	130	60	13th	8th
Cyclopoid copepods										
Oncaea sp.	0.5	3	4	1	2	2	3	1	16th	15th
Corycaeus sp.	0.5	0	1	0	1	0	0	0	—	—
Sapphirina sp.	0.5	0	1	0	1	0	0	0	—	—
Saphirella	0.5	1	1	0	0	0	0	0	15th	16th
Caligoid copepods	3.0	0	1	0	0	0	0	0	—	—
Hyperiid amphipods										
Hyperia bengalensis	0.2- 2.5	282	24	238	29	0	10	0	1st	1st
Gammarid amphipods	1.0	1	1	1	0	0	0	1	—	20th
Isopod larvae	—	0	2	0	0	0	0	0	—	—
Mysids	2.0- 7.0	2	15	15	16	0	0	0	10th	7th
Stomatopod larvae	3.0- 8.0	3	1	1	0	0	0	0	—	17th
Caridean shrimp larvae	0.5-10.0	243	630	330	130	70	214	35	3d	5th
Panaeid shrimps										
Lucifer	3.0-12.0	8	4	10	10	0	0	0	7th	13th
Crab zoea	0.2- 3.0	26	162	55	280	55	65	0	12th	19th
Crab megalops	0.3- 2.0	3	12	0	3	0	0	0	6th	14th
Lobster puerulus	4.0	0	1	0	0	0	0	0	—	—
Lobster phyllosome	—	0	1	0	0	0	0	0	—	—
Insects	1.0	0	0	0	1	0	0	0	9th	9th
Echinoderms										
Echinopluteus larvae	0.2- 1.0	>4,000	>1,000	>2,000	>3,000	—	>100	>1,000	—	—
Holothurian larvae	0.2- 1.5	3	0	2	1	0	0	1	—	—
Ophiuroid larvae	—	3	0	2	0	0	0	0	—	—
Chaetognaths										
Sagitta enflata	4.0-12.0	~120	~180	~150	~350	~900	~440	~600	—	-
S. neglecta	4.0- 8.0	4	30	~100	~ 40	~ 80	~100	~ 100	—	—
S. regularis	3.0- 6.0	0	6	50	10	28	10	30	—	—
Chordates										
Larvaceans	0.5- 3.0	30	36	50	100	35	9	682	17th	—
Fish eggs	0.2- 1.0	26	80	40	55	200	14	60	—	—
Fish larvae	1.0- 5.0	20	22	25	9	—	4	22	—	—

the 24th. Significantly, they were three times more numerous in the surface plankton samples on the 24th (Table 2).

Caridean Shrimp Larvae

Our data suggest an increase in caridean shrimp larvae at the surface after dark, even though many are present in daylight (Table 2). Based on the collections, caridean larvae were more numerous in the plankton than were the forms discussed above, but many were too large to be taken as prey by the silverside (see below). It remains undetermined how many of those individuals in the plankton were, in fact, suitably sized prey, so that numbers in the gut samples cannot be related to numbers in the plankton, as is done above.

Candacia discaudata

The greater numbers of this copepod in the diet of the silverside on 24 March, when it ranked fourth, compared to 23 March, when it ranked eighth, is consistent with its relative numbers in the plankton on these two dates (Table 2). As with other prey of the silverside, the presence of *C. discaudata* in the night collections, and its absence from the day collections (Table 2), probably can be attributed to a diel vertical migration.

Undinula vulgaris

In the samples from 4 to 5 m deep, *U. vulgaris* was equally abundant day and night; however, it was numerous in the surface collections only at night (Table 2). Thus, although this copepod swims at the surface after dark, it seems to be at least a few meters deeper during the day. This conclusion is in agreement with Johnson (1949), who found *U. vulgaris* abundant at or above 2 m only at night and concluded that it descends to deeper water in daylight.

Based on the plankton hauls, *U. vulgaris* was present in similar numbers on both nights—with perhaps more at the surface on 23 March. Consistent with this, it was ranked fifth in the gut contents on the 23d, and sixth on the 24th.

Other Prey

The silverside preyed on many other forms at the time of this study, but in fewer numbers than the above (Table 1). Probably various of these lesser prey, though of secondary importance here, assume major status under appropriate conditions. In general, these other prey have many of the characteristics of the major prey: most are crustaceans or larval forms of other groups, and generally they seem to rise into the surface waters at night, then descend to deeper water during the day (Table 2).

Prey Size

Undoubtedly size is important in determining whether or not a given organism is suitable prey for the silverside. Based on the gut-content analysis, most prey are between 0.5 and 3 mm in their greatest dimension. Nevertheless, other factors are also important. For example, the size range of the abundant larvaceans in the plankton samples was precisely the size range of most prey—0.5 to 3 mm—and yet only a single larvacean was found among the gut contents. Obviously some characteristic of the larvaceans, apart from size, excluded them as prey for the silverside.

BEHAVIOR OF SMALL SILVERSIDE

Limited observations indicate that individuals smaller than about 30 mm behave differently than the larger fish, discussed above. During the day the smaller fish do not school with the larger individuals along the beach; instead, they occur in small schools 1 m or so in diameter that swim in the upper part of the water column 20 m or more away from shore. The fish in these schools appear to be actively feeding, as individuals are continually breaking away from the school, snapping at objects in the water that were too small to be seen by us, and then immediately dashing back to the school—all in one rapid, continuous movement. None of these small active individuals were collected during the day for gut-content analysis; however in the collections offshore at night, in which the 64 larger individuals were collected for the gut-content analysis (Table 1), 5 individuals less than 30 mm long also were taken (3 on 23 March; 2 on 24 March). Significantly, although the guts of all 64 larger individuals contained food, the guts of all 5 small individuals were empty.

These limited data suggest that the small silverside may feed during the day but not at night.

CONCLUSIONS

1. During the day in the Majuro Atoll lagoon silverside larger than 35 mm long assemble in relatively inactive schools along the beaches. These fish do not feed at this time.
2. Shortly after sunset these schools migrate away from shore, following the same route day after day.
3. Once out into the lagoon the schools disperse, and the fish spread out just under the water's surface. They feed throughout the night,

operating as individuals 2 to 4 m apart. Some occur as far as 2 km off the beach.

4. The prey of the silverside are zooplankton, mostly crustaceans between 0.5 and 3 mm in greatest dimension, that occur right at the water's surface after dark. Generally they are species that rise to the surface at night, and descend to deeper waters during the day, and are selected by the silverside from among other organisms of similar size that are not taken.

5. Major prey include a hyperiid amphipod, myodocopid ostracods, the tretomphalus stage of foraminiferans, caridean shrimp larvae, and calanoid copepods.

6. At first morning light, about 1 h and 15 min before sunrise, the silverside begin to concentrate in the shoreward part of their feeding ground. The school continues to develop for about 45 min, then having attained daytime proportions, it moves inshore over the same route it had taken when moving outward the night before. About 20 min before sunrise it arrives at its diurnal schooling site, and the daytime period of inactivity begins.

7. The behavior of silverside less than 30 mm long is in contrast to that of large individuals. Limited evidence indicates that these small fish feed by day and not at night.

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STENELLA COERULEOALBA IN THE EASTERN AND CENTRAL TROPICAL PACIFIC

On the basis of a study of the pigmentation patterns of specimens referred to several nominal species of *Stenella* (*Delphinus coeruleoalbus* Meyen 1833, *D. marginatus* Desmarest 1855 ± 1, *D. euphrosyne* Gray 1846, *D. styx* Gray 1846, and *D. lateralis* Peale 1848), Fraser and Noble (1970) concluded that they should all be included in one species, *Stenella coeruleoalba* (Meyen, 1833). Sampson (1970) summarized North Pacific records of the species and reported a sighting about 1000 miles west of Los Angeles. This note lists seven additional tropical locality records for the species and extends the known range of this distinctively marked small delphinid deep into the eastern tropical Pacific (Fig. 1).

A complete skeleton and external cast in the Bernice P. Bishop Museum in Honolulu, Hawaii, are of an animal captured in the Ala Wai Canal, a brackish canal running through Honolulu behind Waikiki Beach, on 2 March 1958 (Fig. 2). The only previous report near Hawaii is for the type of *Delphinus lateralis* (Peale, 1848), which subsequently was reported to have been lost (Poole and Schantz, 1942). Condylobasal length of the skull of the Hawaiian specimen is 452 millimeters.

On 14 November 1966, Balcomb collected by shotgun a specimen (Fig. 3), 179 centimeters long, with testes 3 centimeters long, at approximately 9° N latitude, 178° W longitude, from a school of approximately 70. Its weakly expressed lateral stripe was not apparent in the water. The complete skeleton, photographs, and external measurements are in the mammal collection of the U.S. National Museum (USNM 395776).

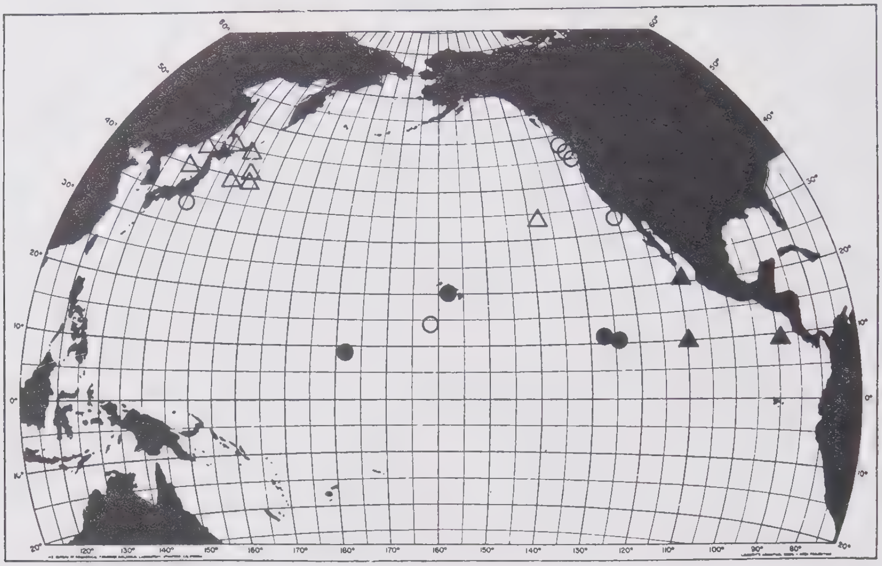
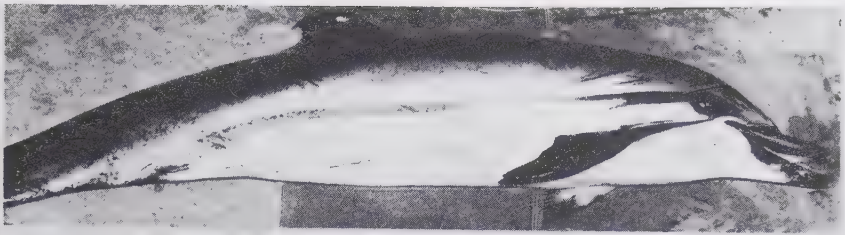


FIG. 1.—*Stenella coeruleoalba* in the Pacific. Circles are specimen localities; triangles are sighting localities. Open symbols are previously published localities, shaded symbols are new localities. Sighting localities in northwestern Pacific are from Sleptsov, 1961; remainder of previously published localities summarized in Sampson, 1970.

A tuna purse seiner captured an immature male on 15 August 1970, at 10° 41′ N, 124° 21′ W. The animal was associated with an aggregation of spotted porpoises, *Stenella* cf. *graffmani* (Lönnberg, 1934), yellowfin tuna, *Thunnus albacares*, and skipjack, *Katsuwonus pelamis*. Craig J. Orange obtained the specimen. This is the southernmost record for a collected specimen in the eastern Pacific. The animal (Fig. 4) was 214 centimeters long and weighed 102 kilograms. A photograph of this specimen appear in Leatherwood *et al.* (1972). The complete skeleton, photographs, and external measurements are in the marine mammal collection of the National Marine Fisheries Service (NMFS), Southwest Fisheries Center, La Jolla, California.

D. W. Rice (personal communication) sighted a group of about 40 animals on 27 February 1965, at 22° 11′ N latitude, 108° 49′ W longitude, during a whale-marking cruise. The following year, on 25 and 26 February, schools of about 200, 70, and seven animals were seen by Rice and Balcomb in the same area, at 21° 59′ N, 106° 54′ W; 22° 12′ N, 107° 32′ W; and 22° 20′ N, 108° 04′ W respectively. A photograph, although slightly out of focus and not here reproduced, allows positive identification, because the spinal blaze and eye-to-anus stripe (terminology of Mitchell, 1970) are clearly visible. On 16 February 1967, Rice and Toshio Kasuya sighted two groups of about 40 and 10 animals, at 22° 10′ N, 108° 13′ W and at 22° 10′ N, 108° 09′ W. These previously unpublished series of sightings near the mouth of the Gulf of California were referred to by Sampson (1970) and by Leatherwood *et al.* (1972).

A school of approximately 100 individuals was sighted on 5 December 1971 at 10° 15′ N, 109° 45′ W by W. E. Evans, J. C. Coe, and D. B. Holts aboard the NMFS-chartered commercial tuna seiner *Queen Mary* (see Leatherwood *et al.*, 1972). The weather was clear and the sea was calm. The spinal blaze and eye-to-anus stripe were clearly seen (personal communication from W. E. Evans).



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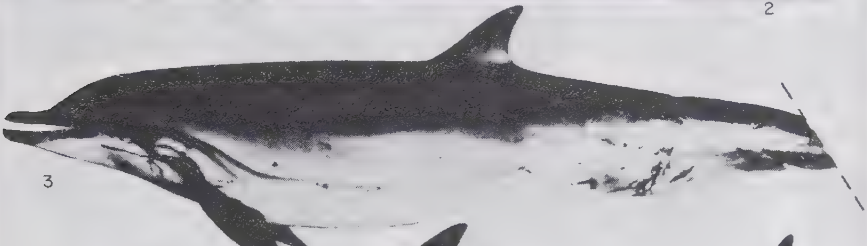

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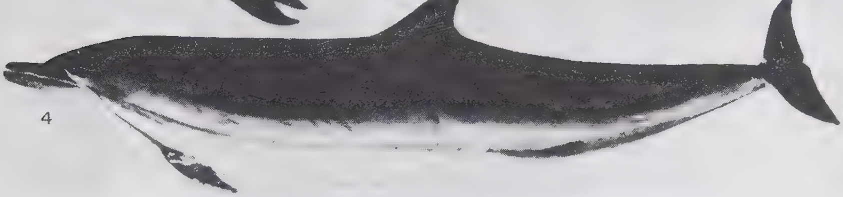

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Fig. 2.—Specimen of *Stenella coeruleoalba* from Hawaii.
Fig. 3.—Specimen of *Stenella coeruleoalba* from 9° N, 178° W.
Fig. 4.—Specimen of *Stenella coeruleoalba* from 10° 41′ N, 124° W.

On 19 March 1972, 300 to 400 animals were sighted at 9° 36′ N, 89° 29′ W by J. M. Coe, a NMFS observer aboard the tuna seiner *John F. Kennedy*. This is the southernmost and easternmost record for the species in the eastern Pacific. On 20 May 1972 at 11° 14′ N, 127° 47′ W, two individuals were captured by the seiner *Carol S* from a school of approximately 1500. No tuna were captured with the cetaceans. The complete frozen specimens, a male and a female, have been acquired by the Los Angeles County Museum.

The now-evident wide distribution across the tropical Pacific strengthens the view that the northern and far-southern populations of this species are conjoined and thus confirms the synonymy adopted by Fraser and Noble (1970).

We thank D. W. Rice, T. Kasuya, C. W. Orange, W. E. Evans, J. M. Coe, and D. B. Holts for allowing us to include their unpublished observations. Spencer Tinker, Director of the Bishop Museum, kindly allowed one of us (Hubbs) to borrow the Hawaiian specimen for study and also furnished the photograph used for Fig. 2. J. S. Leatherwood and D. R. Patten allowed us to include the collection record for the two specimens very recently acquired by the LACM. Studies of this species by Hubbs were supported by grants from the National Science Foundation.

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7316

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INCONSISTENCIES IN LOCATING THE FIRST ANNULUS OF PACIFIC SARDINES[1]

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A special scale reading session designed to bring together old and new scale readers to compare the criteria for estimating the first annulus in sardine scales (L_1), examined scales collected from the 1941 through 1962 sardine landings. Estimates of L_1 by the original readers were consistently lower than those of the newer readers. The reported increase in Pacific sardine length at the formation of first annulus appears to be due to a change in the older reader's criteria for the position of the first annulus. In addition, there was a gradual replacement of the older readers by newer ones who consistently read higher and thus overestimated L_1. Hence, it appears that there was no real change in sardine growth rates during these years.

INTRODUCTION

Walford and Mosher (1943a, 1943b) validated the use of scales for estimating the age of the Pacific sardine and set criteria for the scale annulus. In 1960, I suspected the sardine scale readers were not strictly following the criteria in locating the first or innermost annulus. The radius of this annulus is used to estimate the L_1 (defined as (i)) the calculated length of the fish at the end of the first year of life (Marr 1960), or (ii) the calculated length of the fish at the time of formation of the ring in the first year of life (Phillips 1948a). From information obtained on the time of annulus formation on known-age sardine (Kimura and Sakagawa 1972) the second definition is recommended.

The L_1 is one of the basic measurements for estimating growth (Phillips 1948b). It has also been used as a parameter to separate subpopulations (Felin 1954), and to support certain hypothesis about the population (Marr 1960). The importance of the parameter warranted that a study be made to determine if scale readers were changing L_1 estimates by mislocation of the first annulus.

Preliminary analysis of the scale-age data and rereads of a random number of scales for the 1941–42 through 1961–62 seasons indicated that the only conclusive way to settle the matter was by direct comparison of scale reading between the original scale readers and the readers then in tenure. This report describes the results of the comparative scale reading.

MATERIALS AND METHODS

On March 25–29, 1963, the three original scale readers and the circa 1963 scale readers met at Hopkins Marine Station, Monterey, California, to determine whether the latter readers were following the original

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readers' criteria in reading Pacific sardine scales. Since the three original readers had been away from such work for so long, certain steps were taken to ensure their ability to read scales in the same way as they did during their tenure. For practice they were sent, 4 months before the formal meeting, 100 scale slides which each had read and recorded during his tenure. They also practiced as a group prior to the formal meeting, and a test was carried out for consistency in aging with 60 slides selected from the 1941–42 through 1943–44 season. They agreed about 88% of the time, which compared favorably to the 80–90% agreement when they were in tenure. The 1963 readers did not practice but were told to read in the same manner as they were doing.

At the formal meeting each reader read independently the same preselected scales from 105 scale samples of fish taken in the San Pedro, California, fishery. The pre-selected scales were those selected originally by the historical scale readers (as recorded on scale cards) and were distinguished from the others for the present test by encircling with a glass-marking pen. The remaining scales on the slide were left in view to aid each reader in his evaluation of the annulus.

Other test scale readings included individual readings on the same slides but each individual selecting a scale of his choosing, two-separate group readings on the same slides, and a final reading whereby all seven readers together read a series of slides. All showed the same trend as is described for the test in the present report.

After viewing the scale on a scale projector, the reader recorded the radii of all annuli, and also the margin of the scale on a scale card. The reader went through the same procedure for each of the 105 slides; five slides for each of the 21 seasons from 1941–42 through 1961–62, the same method used and described by Felin and Phillips (1948). The back-calculated lengths of the fish at various annuli were obtained with a nomograph by the method of Phillips (1948a).

The average L_1 values were calculated for the original and the 1963 readers, respectively, and the results compared. The average L_1's from the historical data used to prepare the age and length reports for the Pacific sardine reported by Wolf (1961) were also calculated for comparison.

RESULTS

A graphic comparison of L_1 estimations by seasons for both groups of readers and the historical readers shows that the L_1 estimates of the original readers were consistently lower than those of the 1963 readers (Figure 1). The historical average L_1 had a positive trend with time but the other two did not.

DISCUSSION

A comparison of the scale readings shows that the 1963 scale readers were not following the criteria of the original readers. Therefore, the average L_1 values which were used as a basic measurement for estimating growth, to separate subpopulations, and to support certain hypothesis about the population needed to be reexamined. For example, Marr (1960) found a positive trend with time in the L_1 values for the year-classes 1934 through 1955 for the fishery at San Pedro. He assumed that the increase in length of L_1 was caused by biological or

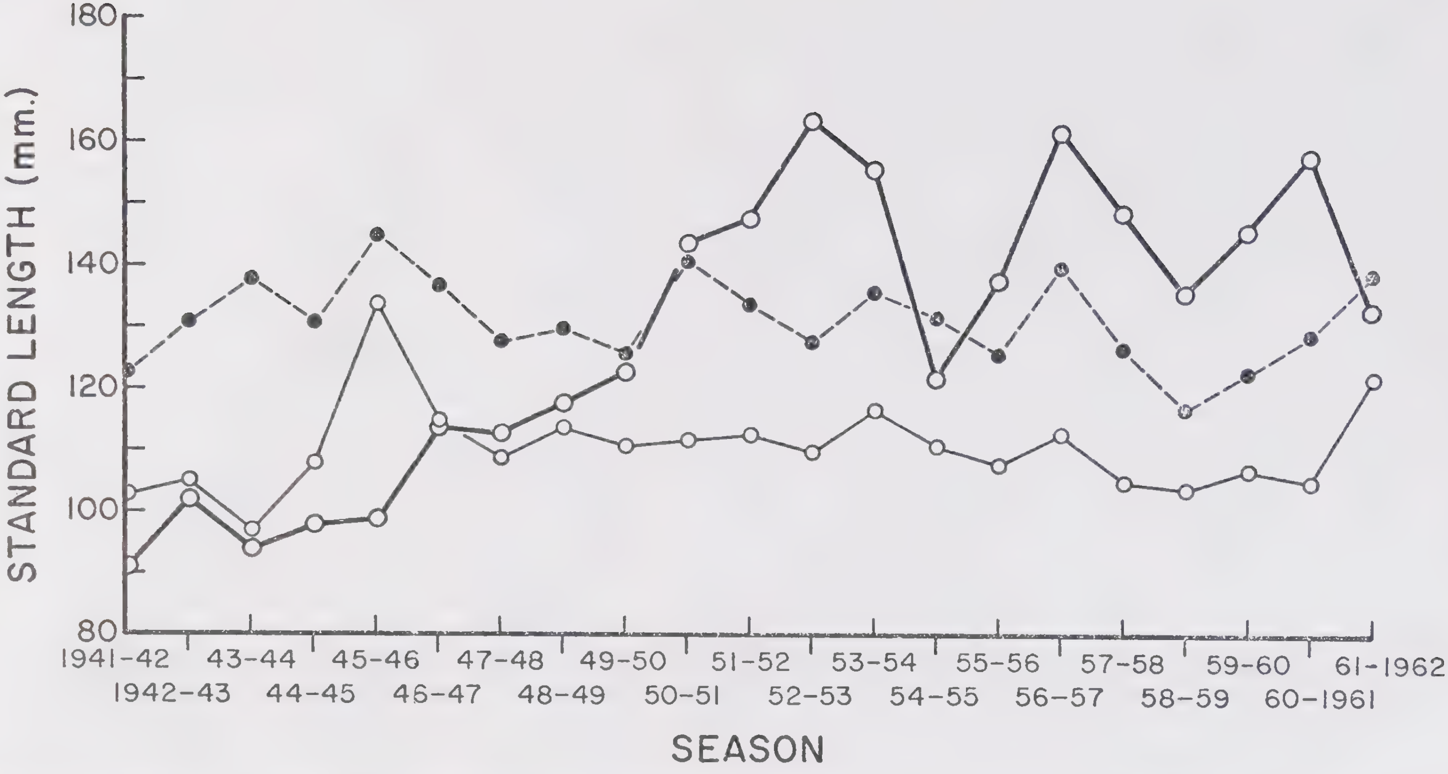

FIGURE 1. Comparison of calculated sardine lengths in mm at first scale annulus (L_1)-in time. The heavy line connects averages of L_1's from scales of five fish in each season as they were historically read. The light line connects the averages of L_1's of the three original scale readers and the dashed line connects the L_1's of the four 1963 readers.

environmental factors which affected the Pacific sardine; but, this study indicates the change in L_1 was the result of scale reader bias.

The consensus of opinions among scale workers is that consistency among a group of readers, or the presence of experienced readers guarantee results comparable to past results. However, there were two experienced readers present at the time the historical L_1 estimation began its abrupt increase in the mid-1940's. The present study indicates that while the 1963 readers were consistent among themselves, their criteria were inconsistent with those of the original readers. Kimura and Sakagawa (1972) concluded on the basis of a comparison of L_1 of known age sardine with the average L_1 of fish aged by the early and recent scale readers that the early readers' L_1 estimations were closer to that obtained from the known age fish.

The results obtained here indicate a need for some kind of standard or length-by-age values to serve as a reference to the readers in obtaining back-calculated length measurements. A suggested standard is a series of random, stratified-by-age scales, i.e., O-, I-, II-, III-, . . . n-year-old fish scales, preferably selected from the time period when the validators of the scale (otolith and any other bony structures used in aging) method were in tenure, or were used by the validators as the basis of their study. For the sake of simplifying comparative readings and as assurance that the same scale will be read at all times, the initial readers of the standard series of slides should circle the selected scale with a marking pen. Similarly, the slides read routinely during a season should also be circled by the initial reader so that both a reader and the checker can be certain to have examined the same scales.

The presence of such a set of standard slides probably would (i) assure continuity in the manner of the scale interpretation by the original validators of the scale or any other method used in estimating fish age, (ii) counteract and monitor the effect of dominance of any individual scale reader, and (iii) deter the occurrence of similarly costly mistakes as illustrated in this study.

CONCLUSIONS

The circa 1963 scale readers have not been reading like the original readers and, apparently, have not been following the same criteria in estimating the L_1. The L_1 value change in time resulted from scale-reader subjectivity and was not caused by biological or environmental factors.

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Determination of Fat Content in Fish with a Nontoxic, Noninflammable Solvent

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Korn, S., and D. Macedo. 1973. Determination of fat content in fish with a nontoxic, noninflammable solvent. J. Fish. Res. Board Can. 30: 1880–1881.

An inexpensive method to determine the fat content in fish using a nontoxic, noninflammable solvent is described. A preweighed, dry, ground fish sample is put in a chromatography column with anhydrous sodium sulfate. One hundred milliliters of monofluorotrichloromethane (MF Freon, refrigerant-11) is poured through the column and the effluent collected in a preweighed beaker. After evaporation of the solvent on a hot plate and cooling in a desiccator, the fat is weighed and fat content calculated. Calculations for samples from two species were similar to those obtained by Association of Official Agricultural Chemists fat extractor method. The column method compares favorably with the fat extractor concerning cost and time.

Korn, S., and D. Macedo. 1973. Determination of fat content in fish with a nontoxic, noninflammable solvent. J. Fish. Res. Board Can. 30: 1880–1881.

Les auteurs décrivent une méthode peu dispendieuse permettant de déterminer la teneur en gras du poisson à l'aide d'un solvant non toxique et ininflammable. Un échantillon de poisson, préalablement pesé, séché et moulu, est placé dans une colonne à chromatographie avec du Na_2SO_4 anhydre. On verse dans la colonne 100 ml de monofluorotrichlorométhane (MF Freon, réfrigérant-11), et on recueille l'effluent dans un becher préalablement pesé. Après évaporation du solvant sur une plaque chauffante et refroidissement dans un dessicateur, on pèse la graisse et on calcule la teneur en gras. Les auteurs comparent la méthode de la colonne avec celle de l'extracteur des graisses donnée par l'Association of Official Agricultural Chemists et arrivent à des résultats semblables. Sous le rapport à la fois du coût et du temps requis, la méthode de la colonne se compare favorablement avec celle de l'extracteur des graisses.

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THIS report describes an inexpensive column extraction procedure for determining fat content in fishes which utilizes a nontoxic and noninflammable solvent. Toxic, inflammable solvents such as ether, chloroform, and benzene are used in other methods: mainly by extraction by Soxhlet-type apparatus (Goldfisch Fat Extractor[1], Horowitz 1965) and shaking the ground sample with a solvent (Folch et al. 1951; Bligh and Dyer 1959).

Fish samples are dried at 70 C for 96 hr and reduced to a coarse granular consistency by repeated cutting with scissors or by electric blending. The dried samples and the 150-ml fat collection beakers are stored in a desiccator for use.

Chromatography columns (20 × 400 mm) with a size 2 teflon stopcock fused just below the fritted disc are prepared for extraction by inserting 20 g anhydrous sodium sulfate (Na_2SO_4) into the bottom of the column. A weighed dry fish sample mixed with 40 g Na_2SO_4 is poured into the column, followed by another 20 g of Na_2SO_4. One hundred milliliters of monofluorotrichloromethane (MF Freon, refrigerant-11) is poured into the column and the effluent collected with dry preweighed 150-ml beakers. Just after the effluent starts passing through the column, the valve is closed for a 1-hr retention period. This stops the flow and allows for a soak period. The extract is collected and the contents are concentrated on a hot plate (40–50 C) in a fume hood to near dryness (30–60 min). The beakers are then dried for 1 hr in a 70 C oven and cooled in a desiccator. After reweighing the beakers, the fat weight and the fat concentration are calculated.

To compare this method with an established procedure, dried fish were blended and divided into 47 2-g samples (striped bass *Morone saxatilis*) and 35 4-g samples (Pacific herring, *Clupea harengus pallasi*). Half of the samples (six per trial) were run on a Labconco–Goldfish fat extraction apparatus using the A.O.A.C. method (Horowitz 1965). The other half (five to six per trial) were run simultaneously using the described method.

Two way analysis of variance of the data showed that the dried fish did not change in fat content over the test period ($P \leq 0.05$). This allowed us to combine values from different trials to compare results. Similar analysis also showed that results from the column method did not differ from the soxhlet procedure with 2- and 4-g samples ($P \leq 0.05$).

The percents fat obtained with the two methods were:

Method	Sample weight (g)	%Fat
Goldfisch fat extraction		
Striped bass (24)[a]	2.38±0.34[b]	18.2±0.34
Pacific herring (18)	4	7.84±0.20
Column fat extraction		
Striped bass (23)	2	18.1±0.64
Pacific herring (17)	4	7.87±0.17

[a] Number of fish.
[b] Mean and one standard error.

The column method compares favorably with other methods concerning labor and expense. It takes 3–4 hr from start to finish as compared with 6–7 hr for the Goldfisch apparatus and 24 hr for Folch's method. Cost for the column method is about $100 to set up equipment to run six samples simultaneously, and for the fat extractor about $990 plus the cost of extraction solvents. The column method also has applications in extracting fat from other samples, e.g. wet fish tissues, food stuffs, and mammalian tissue (Hesselberg and Johnson 1972).

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[1] Reference to trade names in this paper does not imply endorsement of commercial products.

7318

MFR PAPER 979

Seasonal and Geographic Characteristics of Fishery Resources, California Current Region: IX. Inshore Sportfishes

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INTRODUCTION

It has been stated that the sports fishery in California "...is probably the most dynamic of its kind in the world and is currently—not merely *potentially*—yielding some very high returns." (Mathews, 1971). More than one million anglers are estimated to be contributing to that yield each year. Talbot (1969) reported that in 1965 more than two million anglers fished on the Pacific coast spending almost $300 million on this sport. Although there was no breakdown by states, he added, California, because of its population, better weather and species available undoubtedly enjoys a big share of the fishery's effort and catch. The majority of fishermen seldom go beyond the sight of land and many fish only from shores, jetties, and piers.

A subject of recent concern has been at least 12 inshore species of fish for which this great number of anglers are always seeking. The catches of many of these species have been declining by numbers and sizes with only a slight increase in anglers. The fish for which such concern is expressed are: the California halibut, the white sea bass, the halfmoon, the California yellowtail, the ocean whitefish, the California barracuda, the California bonito, the sheephead, the California black sea bass, the California corbina, the spotfin croaker, and the yellowfin croaker (Table 1).

The biological and oceanographic surveys of the California Cooperative Oceanic Fisheries Investigations (Cal COFI) were originally directed toward the eggs and larvae of massive oceanic fish populations like the Pacific sardine (Kramer and Smith, 1971c) and its ecological associates, the northern anchovy (Kramer and Smith, 1971a), the jack mackerel (Kramer and Smith, 1970a), the Pacific mackerel (Kramer and Smith, 1970b), the Pacific hake (Kramer and Smith, 1970b), the rockfishes (Kramer and Smith, 1971b), the Pacific saury (1970b), and the characteristics of their environment, particularly the seasonality of their planktonic food and the water temperature. Unfortunately, the density of stations was not sufficient for the smaller, more dispersed populations characteristic of the sportfishes in general.

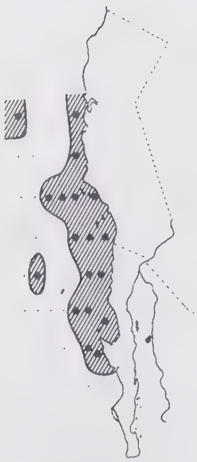
As yet, our data on these inshore sport fish species are not sufficient to determine the reasons for the decreases. However, there are enough data to reasonably describe and depict their seasonal and geographic distributions (Table 2, Figure 1a-i) which, combined with future research, may enable us to determine the reasons for the decreases. The distributions are based on

Table 1.—Selected species and/or family groups (see text) of inshore sport fishes in the California Current region.

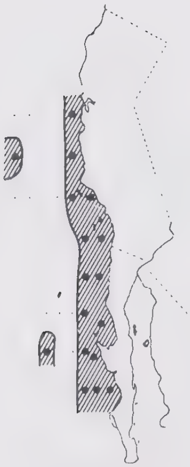
Family		Species	
Scientific name	Common name	Scientific name	Common name
Sciaenidae	Croakers	*Cynoscion nobilis*	White sea bass[1,2]
		Menticirrhus undulatus	California corbina[2]
		Roncador stearnsi	Spotfin croaker[2]
		Umbrina roncador	Yellowfin croaker[2]
		Cheilotrema saturnum	Black croaker
		Genyonemus lineatus	White croaker or kingfish
		Seriphus politus	Queenfish
Serranidae	Basses	*Stereolepis gigas*	Sea bass[2]
		Paralabrax clathratus	Kelp bass
		P. nebulifer	Sand bass
		P. maculatofasciatus	Spotted bass
		Mycteroperca sp.	Groupers
Labridae	Wrasses	*Pimelometopon pulchrum*	Sheephead[2]
		Oxyjulis californica	Señorita
		Halichoeres semicinctus	Rock wrasse
Bothidae	Left-eyed flounders	*Paralichthys californicus*	California halibut[1,2]
Scorpidae	Halfmoon	*Medialuna californiensis*	Halfmoon[1,2]
Carangidae	Jacks	*Seriola dorsalis*	California yellowtail[1,2]
Branchiostegidae	Tilefish or blanquillo	*Caulolatilus princeps*	Ocean whitefish[1,2]
Sphyraenidae	Barracudas	*Sphyraena argentea*	California barracuda[1,2]
Scombridae	Mackerels	*Sarda lineolata*	California bonito[2]

[1] Fish whose larvae have been identified to species. All others are assigned to and grouped within their families with look-alike larvae of species from which they have not been distinguished (see Table 2)

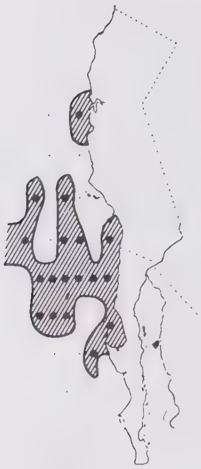
[2] Fish of concern in this report



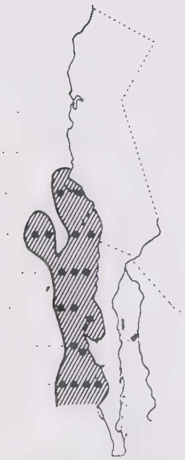
a WHITE SEA BASS
FEBRUARY



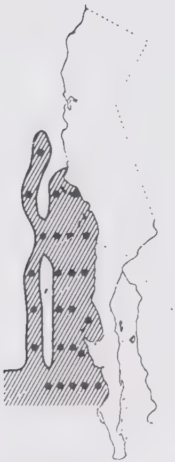
b CALIFORNIA HALIBUT
FEBRUARY & JULY



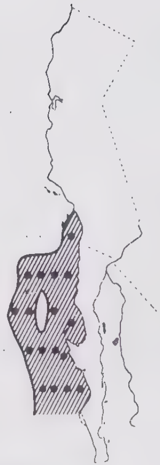
c. HALFMOON
JULY



f. CALIFORNIA BARRACUDA
JULY



g. CROAKERS
JANUARY & AUGUST



h. BASSES
AUGUST

the enumerations of fish larvae collected in the plankton tows of CalCOFI[1]—each occurrence in any survey conducted from 1955 to 1960 (1956-59 for wrasses and 1956-60 for basses).

The larvae of six of the species of concern have been identified and enumerated and five have been assigned to their families with their look-alikes of the same or different genera (Table 1). The California bonito is not discussed here because there are so few larvae in our collections—although the commercial catch attests a rather large population. The reasons for their absence in the plankton tows are not known. The six known species are the barracuda, the white sea bass, the halibut, the yellowtail, the ocean whitefish, and the halfmoon. The larvae assigned to and grouped with others in their families are those of the sheephead of the wrasse family (Labridae), which includes the señorita and the rock wrasse—neither one considered a sport fish; the black sea bass of the bass family (Serranidae), which includes the kelp bass, sand bass, spotted bass, and two species of groupers from Baja California (sometimes known from San Diego County)—all considered sport fish; the spotfin croaker, yellowfin croaker, and corbina of the croaker family (Sciaenidae), which includes the black croaker, white

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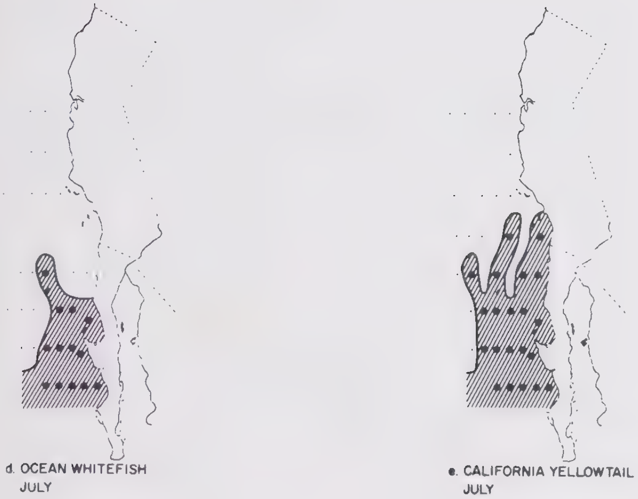
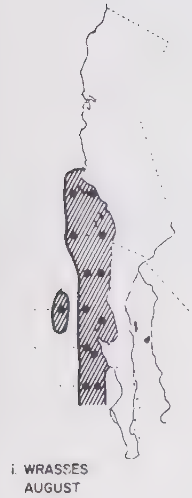
[1] Organizations, area of investigation, and treatment of the data were presented by Kramer and Smith (1970a).



d. OCEAN WHITEFISH
JULY

e. CALIFORNIA YELLOWTAIL
JULY



i. WRASSES
AUGUST

Figure 1a-i.—Regions of spawning of selected species or families of inshore sport fishes in the California Current region 1955-60 (1956-59 for wrasses, 1956-60 for basses). Each circle represents the total number of occurrences in each pooled area (see Kramer and Smith, 1970a). The months designated are those of peak spawning for the fishes depicted (see Table 2 for seasons).

croaker or kingfish, and the queenfish—all considered sport fish. (Note: the white sea bass listed above as one of the known larva species is also a member of the croaker family.)

SEASONAL AND GEOGRAPHIC DISTRIBUTIONS

Seasonal

All of the species except the white sea bass have their peak spawning in July or August. The croakers and the halibut also have peak spawnings in January and February, respectively; white sea bass peaks only in February.

Inshore-offshore

All of the species are inshore and offshore spawners except the halibut and the wrasses, which spawn only inshore.

North-south

Almost all of the species are chiefly southern spawners except halibut and white sea bass, whose spawning ranges extend northward, probably the entire length of California; southward, the halibut spawns the entire length of Baja California, and the white sea bass is delimited to Punta Eugenia. Ocean whitefish and the yellowtail are exclusively southern spawners. The only records we have of yellowtail larvae off southern California are for 1957 (Figure 1e). Part of that year was included in the so-called warm years—mid-1957 through 1959. The halfmoon is delimited from Point Conception, California, to Punta Eugenia, B.C. The barracuda, croakers, and wrasses spawn from Point Conception southward. The basses spawn from San Diego southward.

RESEARCH REQUIRED

NMFS now has the responsibility for the study of all marine fishes and fisheries, recreational and commercial. The management of recreational fisheries will require additional studies of the target species; to better monitor the catch, bigger samples of the landings will be needed. Competition between the sport and commercial fishing industries, the international character of sport fish distributions, and the ill-defined management objectives for recreational fisheries all pose problems to be solved by fishery scientists in the near future.

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Table 2.—Seasonal and geographic spawning of selected species or families (see text) of inshore sport fishes in the California Current region, 1955-60.

Larva species	Spawning months (season)	Peak spawning months[2]	Area of spawning[1]				Geographical delimitation[1]		
			California		Baja California				
			Onshore	Offshore	Onshore	Offshore	Seaward	Northward	Southward
Differentiated									
White sea bass	January-March	February	×	×	×	×	Yes	No	Yes
California halibut	January-April June-September	February and July	×	—	×	—	Yes	No	Yes
Halfmoon	June and July	July	×	×	×	×	Yes	Yes	Yes
Ocean whitefish	June-August	July	—	—	×	×	Yes	Yes	No
California yellowtail	July-August	July	[3]	—	×	×	Yes	Yes	No
California barracuda	June-August	July	×	×	×	×	Yes	Yes	No
Undifferentiated (grouped to families)									
Croakers (including corbina, spotfin croaker, yellowfin croaker)	January-March June-October	January and August	×	×	×	×	Yes	Yes	No
Basses (including giant black sea bass)	July-October	August	×	—	×	×	Yes	Yes	No
Wrasses (including sheephead)	July-October	August	×	—	×	—	Yes	Yes	No

[1] See Figure 1a-i.
[2] Also see Figure 1a-i.
[3] Onshore California only in 1957 (see text).

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7319

REQUIREMENTS OF FISHERY SCIENTISTS FOR PROCESSED OCEANOGRAPHIC INFORMATION

by R. M. Laurs

According to information gathered by the Food and Agriculture Organization of the United Nations, 1970 world production of marine fish and shellfish amounted to 68.4 million metric tons. Historical records of world fish catches show that the catch has increased steadily each year for the past 30 years. For example, total world catch in millions of metric tons of marine fish and shellfish was about 16.6 in 1948, 27.0 in 1958, and 54.7 in 1968 (Figure 1).

In recent years a number of estimates have been made of how much food the ocean can produce on a sustained basis (Finn, 1961; Graham and Edwards, 1962; Meseck, 1962; Pike and Spilhaus, 1962; Schaefer, 1965 and others). These estimates have been based on extrapolation from recent trends in catch or fishing patterns and calculations based on food chain dynamics. Those based on extrapolation from recent trends in catch appear to give estimates much below those of the latter; however, the processes governing ocean productivity are imperfectly understood and much further study is needed to refine estimates now being made. Nevertheless, the present consensus among fishery scientists is that the production from the sea can be increased significantly, perhaps by a factor of 3 to 5 times that now being produced (Johnson, 1971). It is expected that the greatest increases in catch will come largely from the pelagic plankton-eating fishes (Crutchfield, 1967).

The ultimate amount of food that is harvested from the world oceans on a sustained basis will depend on 1) proper systematic scientific management of the world fishing resources, and 2) improved fishery technology, notably an increase in efficiency of fishing operations through improvement of present methods and development of new and economical harvesting techniques.

For proper scientific management of ocean fisheries it will be necessary to determine the optimum harvest, the traditional criterion of which is maximum sustained yield, for each fishery. This requires an understanding of the interrelationships among 1) population size, 2) fishing intensity, and 3) the environment. Fluctuations in the catch of a population depend on 1) the abundance of the population, 2) its availability to capture, and 3) the amount of fishing. There are means to measure changes in the amount of fishing effort and account for its effects on indices of apparent abundance (Gulland, 1964). However, variations in true abundance and availability (Marr, 1951) are difficult to identify, measure, and understand.

Fish populations are affected by artificial causes, i.e., overfishing, water pollution, etc. However, the primary cause for changes in the availability, and in most cases for abundance of fish populations are from responses of populations to changes in their environment (several authors, notably Sette, 1961 and Uda, 1961).

Fisheries Oceanography

Fisheries oceanography is the study of oceanic processes affecting the abundance and availability of ocean fishes and encompasses the disciplines of oceanography, biology, and meteorology. The goal of fisheries oceanography is to forecast accurately the changes in abundance and availability of fishes based on a fundamental knowledge of the interplay of pertinent atmospheric, oceanic, and biological processes. Fishery-prediction also requires input from population dynamics studies.

The chain of events which affects and controls the marine environment begins with the atmosphere. Changes in the atmospheric pressure field cause variations in wind stress which affect the surface circulation through changes in the velocity, depth, and breadth, and a multitude of other features of ocean currents. Currents affect the distribution of organisms at all trophic levels and, along with winds, determine the nature and strength of refertilization processes of ocean surface waters. The replenishment of surface waters affects primary biological production which, in turn, affects secondary production at each trophic level up to the fishes, with varying lags in time and space. The dynamic air-sea interaction processes which influence the heat-balance of the ocean-atmosphere system also result in marked fluctuations in the marine environment which directly affect the distribution and abundance of marine fishes.

Fishery scientists and oceanographers do not have sufficient understanding of the complex interplay of atmospheric, oceanic, and biological processes as they cause fluctuations in the availability and abundance of fishes to construct quantitative models for forecasting such fluctuations. Up to now, work has been mostly descriptive in nature, but the understanding of the complex interrelationships involved has increased and the possibility of quantifying the results and applying these to fishery prediction models is closer at hand.

For the most part, fishery oceanographers have concentrated on describing the oceanic circulation, attempted to associate physical, chemical, and biological parameters of the ocean with the occurrence of fishes, and documented and interpreted changes in the distribution and abundance of the fishes in relation to changes in these parameters.

No attempt will be made in this paper to describe the efforts of fisheries oceanography or summarize the results. For this the reader is referred to the following publications: Blackburn et al., 1962; Blackburn, 1965; Johnson, 1962; Laevastu and Hela, 1970; Owen, 1968; Sette, 1955, 1956, 1960, 1961; Schaefer, 1961; and Uda, 1961.

General Considerations of Oceanographic Data Requirements by Fishery Scientists

Before detailing the requirements of fishery scientists for processed oceanographic information, there are two general points that should be considered. Oceanography has provided knowledge of average conditions in the ocean and the processes maintaining them in equilibria. However, average conditions are rarely encountered in reality and its is the variations from average ocean conditions that affect the abundance and availability of marine fishes. Much of the effort of the fishery oceanographer is directed toward ". . . studying the changing sea rather than the equilibrium ocean and in studying the biological consequences of the changes at various trophic levels" (Sette, 1961). For his studies then, the fishery oceanographer requires data in both climatological and synoptic time scales.

Secondly, while there are many oceanographic measurements that could be used in studies to understand the effects that varying environmental conditions have on the abundance and availability of fishes, many of these measurements require specialized equipment found only on oceanographic research vessels. However, observations from research vessels usually lack both the synopticity and continuity which are necessary in fisheries oceanography studies. Therefore, it is often necessary to deduce what is desired to be known from something else that is measured in the ocean over sufficiently large time and space scales on a routine basis. For example, information on variations in ocean circulation are extremely important to the fisheries oceanographer, as well as other oceanographers; but rather than having current measurements available to him, he attempts to deduce circulation patterns from variations in distribution of ocean temperature or differences in sea level.

In the sections that follow only those variables which are available, or could be available in the near future, on a routine basis, are discussed.

Sea Surface Temperature

Ocean temperature is one of the most important and universally employed oceanographic measurements in fisheries oceanography and in fish scouting operations. Temperature is significant in marine fisheries because of the direct effects it has on the biology of fishes and because it is a most useful indicator of other prevailing or changing ecological conditions in the ocean. Not only the actual temperature, but its variations in time and space, especially its horizontal and vertical gradients, are important in evaluating the direct and indirect effects that temperature has on marine fisheries. Temperature is the most easily observed variable in the marine environment, and sea surface temperature data are relatively available over large areas of the oceans historically and on a continuing basis. Consequently, much attention has centered on studies of the distribution and abundance of marine fishes in relations to sea surface temperature.

Fishes and other marine life have preferred temperature ranges, and temperature usually sets the limits of distribution of marine organisms (Moore, 1958 and others). The optimum temperature range for distribution and fishing of tuna species, as adapted from Uda (1957) by Laevastu and Rosa (1962), is given in Figure 2. Laevastu and Hela (1970) and Uda (1957) give optimum temperature ranges for several commercially important marine fishes. Sullivan (1954) summarized the findings of various workers on the effects of temperature on the movement of fish, and on the influence of temperature on the distribution of fish, and discussed the role of the receptor mechanism in the temperature response in fish.

In addition to the role that temperature plays in the distribution and availability of fishes, it also affects abundance through its influence on spawning (Ahlstrom, 1959 and many others), survival of larvae (Murphy, 1961 and many others), feeding (Komarova, 1939), and growth (Taylor, 1958 and others). Mass mortalities of fish and other marine life have also reported to have been caused by extreme variations in temperature (Galloway, 1941). Temperature also influences the migration patterns followed by fish (McGary et al., 1961).

Information on the distribution of sea surface temperature is especially important in predicting and locating good fishing areas. Highest concentrations of tuna and other pelagic fish are usually found where there are large gradients in sea surface temperature and where the optimum temperature zone is narrow (Uda, 1961 and others). By way of a specific example of this effect, Figure 3 shows a sharp jump in catch of albacore tuna associated with a horizontal gradient in sea surface temperature.

In addition to acting directly, sea surface temperature is fundamentally related to many ocean processes which play important roles in determining the distribution and abundance of marine fishes. Knowledge of the distribution of sea surface temperature over large areas is important in the detection and monitoring of ocean currents, water mass boundaries, upwelling zones, and certain air-sea interaction processes which influence the heat-balance of the ocean-atmosphere system.

Need for Additional Data Coverage

In spite of the fact that sea surface temperature measurements are probably the most ubiquitous of all measurements made in the sea, there is still need for increased coverage both in time and space. Sea surface temperature measurements, along with marine meteorological observations, are made by merchant ships, fishing vessels, research vessels, and military vessels. The observations are radioed ashore in real-time and the data are disseminated to users over special teletype circuits. While this is a good and important scheme for obtaining synoptic sea surface temperature information, the distribution of the observations is mainly along shipping lanes and therefore large ocean areas are devoid of observations. Often these areas of scarce data are important fishing grounds, such as the eastern tropical Pacific, south Pacific, Indian Ocean, south Atlantic, tropical Atlantic, and polar regions. Figure 4 shows the number and distribution of sea surface temperature observations made during a 1-week period in the eastern tropical Pacific.

Remote-sensing of sea surface temperature from orbiting satellites (McClain, 1969) and from unmanned telemetering buoys (Howard, 1964) appears to hold great promise for providing more extensive coverage of sea surface temperature measurements. However, the total potential of sea surface temperature measurements from satellites will not be realized by fisheries until sensors are developed which will give measurements in all weather conditions. This will enable ocean temperature measurements to be made from satellites in regions of upwelling and other cloud-covered areas where the world's most important fishing areas are located (Laurs, 1972). Efforts should be stepped up markedly to increase the numbers of synoptic observations of sea surface temperature and other marine variables received from ships at sea, especially fishing vessels which often operate away from main shipping routes.

Requirements for Sea Surface Temperature Information

Fishery scientists require analyses and forecasts of sea surface temperature both in climatological and synoptic scales. Monthly means, seasonal means, and annual means and anomalies for each time scale are used in studies relating large-scale environmental variations to marine fishes and to monitor trends in thermal changes in the ocean. It is desirable to have the information both as analog charts and in a digital format suitable for ADP handling. Figure 5 illustrates monthly mean charts of the distribution of sea surface temperature and anomaly pattern in the northeast Pacific.

There is also great need in marine fisheries for synoptic charts of sea surface temperature which provide information about the short-term fluctuations in ocean conditions. These charts should contain sufficient detail to show local, small-scale features in the distribution of sea surface temperature such as locations of upwelling "fronts" and other horizontal temperature gradients, surface eddies and other "patches" of warm or cool water, etc. Because of low data density and data errors, it is usually necessary to composite data over a period of several days in the preparation of quasi-synoptic charts. However, care should be taken to insure that formulation of the analysis period takes into consideration the speed and magnitude of short-term changes in the ocean in the particular area covered by the analysis.

Synoptic analyses of sea surface temperature are used by fishery scientists in fishery forecasting operations and by fishermen in locating productive fishing areas. Japan has taken the lead in providing fishermen with synoptic sea surface temperature information in the form of charts prepared by the Japan Meteorological Agency and transmitted to fishermen via radio facsimile. Recently the U.S. National Marine Fisheries Service commenced issuance of 7-day sea surface temperature charts via radio facsimile to eastern Pacific tuna fishermen (Laurs, 1971).

Thermocline Topography and Vertical Thermal structure

If temperature limits the horizontal distribution of fishes, then we might expect that it can also limit their vertical distribution. This indeed appears to be true, for variations in vertical thermal structure, notably thermocline topography, affect the distribution and availability of marine fishes (Blackburn, 1963; Dietrich et al., 1959; Laevastu and Hela, 1970; Laurs and Lynn, in preparation; Postuma, 1957 and others); however, comprehensive studies are lacking. Laevastu and Hela (1970) give a schematic example of different depth and temperature preference by different species of tuna in tropical latitudes (Figure 6).

Information on vertical thermal structure is also used by fishery oceanographers in monitoring and evaluating other ecological conditions which affect fluctuations in catches of marine fishes, i.e., nutrient replenishment processes (Brandhorst, 1958), variations in ocean circulation (Cromwell, 1958), air-sea interaction and advective processes affecting heat flux (Roden, 1959) and location of water mass and current boundaries (Roden, 1964; Saur and Stewart, 1967). Figure 7 shows how vertical thermal structure can be used to delineate the outer boundary of the California Current.

Vertical thermal structure is also extremely important in fishing strategy for some pelagic species. For example, purse seining operations for yellowfin and skipjack tunas are more successful in thin mixed layers over thermocline of sharp temperature gradients (Green, 1967). When the thermocline is shallow the tuna do not dive into colder waters below but remain in the seine, whereas when the thermocline is deep the fish can dive under the seine before pursing (Figure 8). Information on the depth of the thermocline can also be used in other fishing operations including 1) setting depth of longlines for different tuna species, 2) setting depth of drift nets for herring and salmon species, and 3) determination of the optimum depth for midwater trawling for pelagic species (Laevastu and Hela, 1970). Information on vertical thermal structure is also important to fishermen who use sonar to locate concentrations of fish because thermal structure effects sonar ranges and sound propagation.

Requirements for Vertical Thermal Information

Like the requirements for sea surface temperature, fishery scientists have need for vertical temperature information on climatological and synoptic time-scales. Information at minimum should include depth of mixed layer and thermocline, and thermocline gradient. It would also be desirable to have information on the depth of various isotherms down to approximately 200 meters depth. The vertical thermal information should be in the form of charts and in a digital format suitable for ADP handling.

Salinity

Salinity per se does not appear to have a direct bearing on the distribution and abundance of marine fishes. Studies have shown that salinities over large ranges have relatively little direct effect on the normal fertilization, development, and hatching of marine fish eggs (Holliday and Blaxter, 1960). Variations in salinity affect the osmotic regulations of fish, but marine fishes for the most part are able to make such adjustments relatively easily (Prosser and Brown, 1962).

Except in some coastal waters where land runoff may be large, salinity variations in the ocean are relatively small. Even so, these variations can be important indications of changes in conditions which play important roles in determining the distribution and abundance of fishes. For example, Seckel and Waldron (1960) related the catches of skipjack tuna in Hawaiian waters to variations in salinity near Oahu which were apparently due to variations in ocean currents. Salinity changes can also be used to delineate current boundaries (see top panel of Figure 7) and to indicate change in water masses or in their stability conditions which affect nutrient replenishment processes (Sverdrup et al., 1942).

Requirements for Salinity Information

Fishery scientists have need for monthly, seasonal, and annual mean charts, and anomalies for each period of surface salinity. With the advent of expendable salinity-temperature-depth-sensors (Danielson, 1972), it may also be possible in the future to obtain subsurface salinity data. It is desirable to have the salinity information in the form of contoured charts and in digital format suitable for ADP handling.

Solar Radiation and Extinction Coefficient

While temperature sets the distributional limits for most fishes, the distribution of fish within their optimal temperature range is generally thought to be determined by the availability of food (Blackburn, 1969 and others). Also, the availability of food is probably the ultimate factor affecting larval fish survival (Lasker, 1963; Saville, 1971) which in turn is a major factor contributing to fluctuations in catches of fishes. It is obviously apparent that information on fluctuations in the distribution and abundance of food for various species of fish would be extremely important in fisheries oceanography; it is equally apparent that such information will probably never be available. However, indices of primary production and secondary production have been developed (Parsons and LeBrasseur, 1968; Sverdrup, 1953) which may provide indirect information on potential food available. Parsons and LeBrasseur (1968) indicate that the following information reported from ships of opportunity, aircraft, etc., and summarized as a monthly mean for each 5° quadrangle would allow prediction of gross variations in primary productivity: 1) solar radiation measurements corrected for cloud cover and reflection, 2) extinction coefficient measured by disposable light meter, and 3) mixed layer depth.

Spectral measurements of ocean color may also be useful in locating areas of high biological productivity since they can be used to determine the amounts of chlorophyll in the ocean. It appears that synoptic measurements of sea surface temperature and chlorophyll deduced from spectral measurements could provide valuable information for locating potential areas of good fishing (Blackburn, 1969). Ocean color can also be used to delineate water masses and trace currents.

It appears quite probable that spectral measurements of back-scattered light from the ocean surface will be made by remote sensing in the near future to provide information on ocean color on a global basis (Clarke, et al., 1969). Fishery scientists could use weekly averages of ocean color information in the form of maps of percent composition by red, yellow, green, and blue wavelengths. The information should also be in a format compatible for ADP handling.

Meteorological Observations

There are a number of oceanographic factors that affect the distribution and abundance of fish which are directly influenced and/or determined by meteorological conditions.

No attempts will be made in this paper to discuss the relations between meteorological conditions and ocean conditions; these are well-treated in many textbooks (e.g., Sverdrup et al., 1942) and papers by Clark (1972), Namias (1960, 1963, 1969, 1970 and others) and others. Likewise, this paper will not discuss the needs of fishermen for marine weather information. The influence of weather on fishing operations is discussed by Kesteven (1953) and Terada (1968).

Meteorological data which are important in fisheries oceanography and fishing operations include most of the synoptic surface marine weather observations which are made by ships at sea: barometric pressure, cloud cover, air temperature, air-sea temperature difference, dew point, wind direction and speed, swell direction and height, and wave direction and height. An example of how meteorological data along with oceanographic and fishery data are being used to examine the interrelations between environmental conditions and the distribution of albacore tuna is shown in Figure 9.

Requirements for Meteorological Information

Fishery oceanographers need analyses of meteorological observations noted above both in climatological and synoptic time scales. It is desirable to have the information in graphical form and in a digital format suitable for ADP handling.

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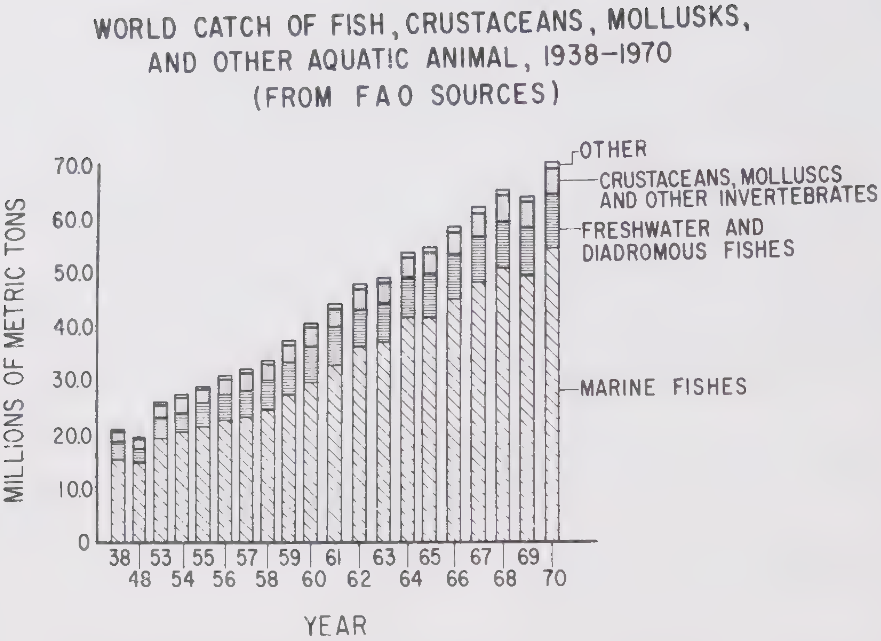

Figure 1.--World catch of fish, crustaceans, mollusks, and other aquatic animal, 1938-1970 (from FAO sources).

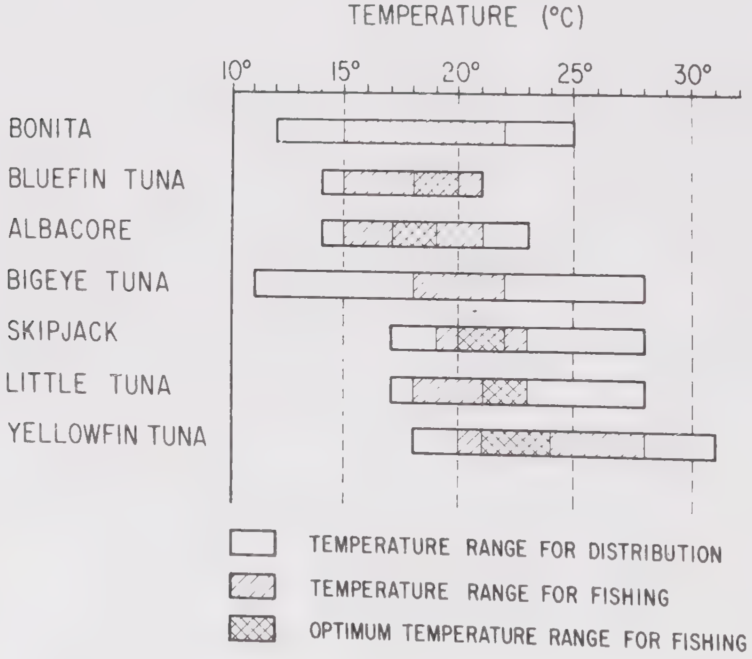

Figure 2.--Temperature range for distribution and fishing of tuna species (from Laevastu and Hela, 1970).

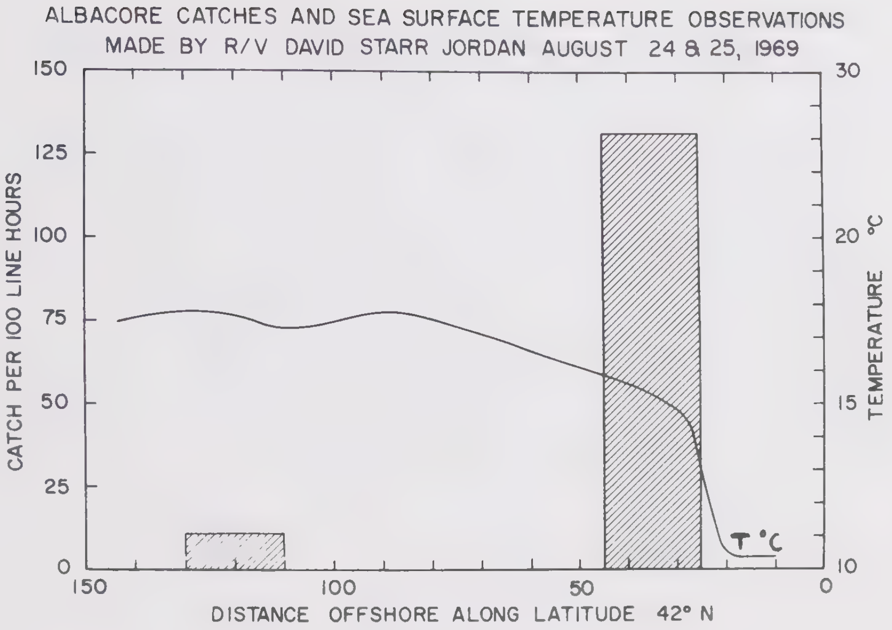

Figure 3.--Albacore tuna catches in relation to sea surface temperature.

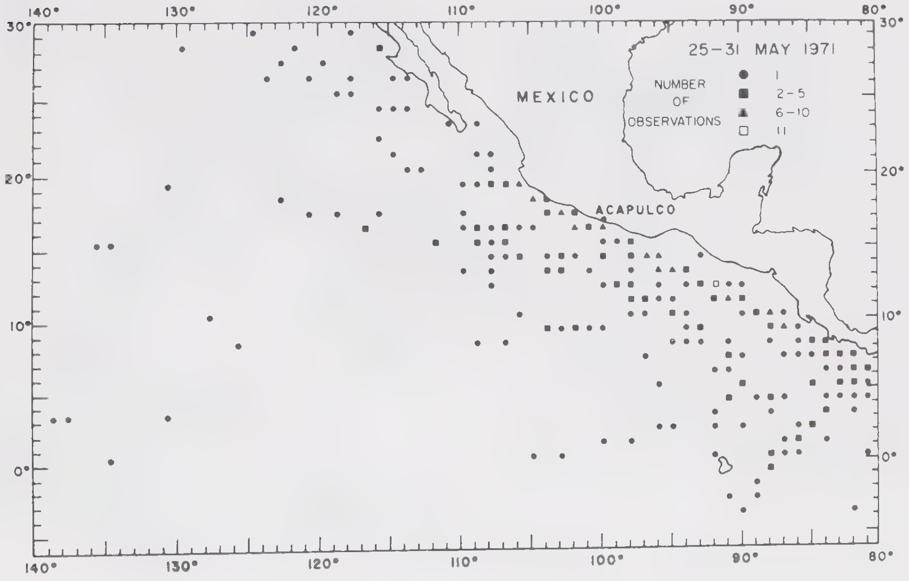
140°
130°
120°
110°
100°
90°
80°
30°
20°
10°
0°
MEXICO
ACAPULCO
25–31 MAY 1971
NUMBER OF OBSERVATIONS
● 1
■ 2–5
▲ 6–10
□ 11

Figure 4.--Number and distribution of sea surface temperature observations made during a 1-week period in the eastern tropical Pacific.

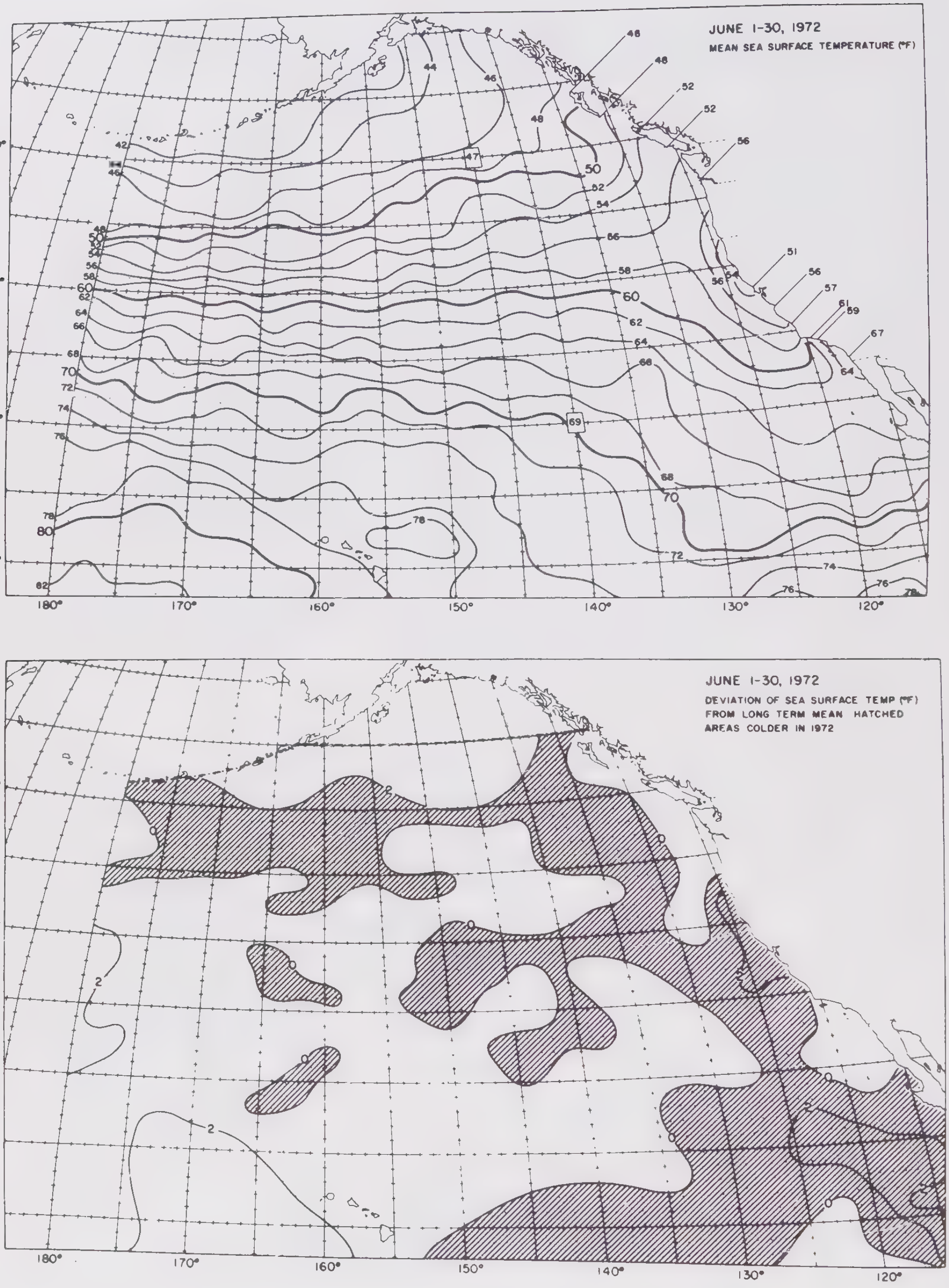
JUNE 1-30, 1972
MEAN SEA SURFACE TEMPERATURE (°F)
JUNE 1-30, 1972
DEVIATION OF SEA SURFACE TEMP (°F) FROM LONG TERM MEAN HATCHED AREAS COLDER IN 1972
50°
40°
30°
20°
180°
170°
160°
150°
140°
130°
120°

Figure 5.--Monthly mean charts of the distribution of sea surface temperature and anomaly pattern in the northeast Pacific (from National Marine Fisheries Service).

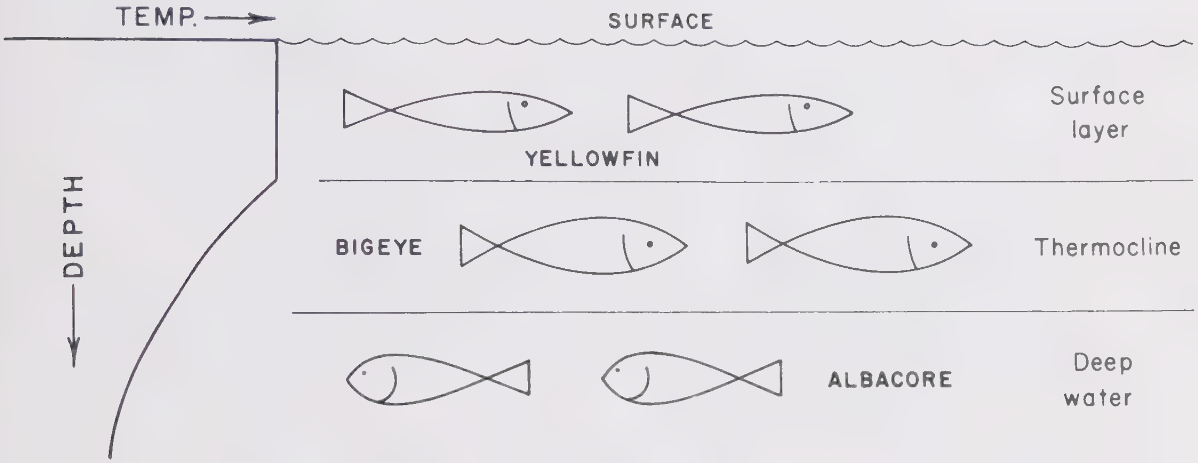
TEMP.
SURFACE
Surface layer
YELLOWFIN
DEPTH
BIGEYE
Thermocline
ALBACORE
Deep water

Figure 6.--Schematic example of different depth and temperature preference by different species of tuna in tropical latitudes (from Laevastu and Hela, 1970).

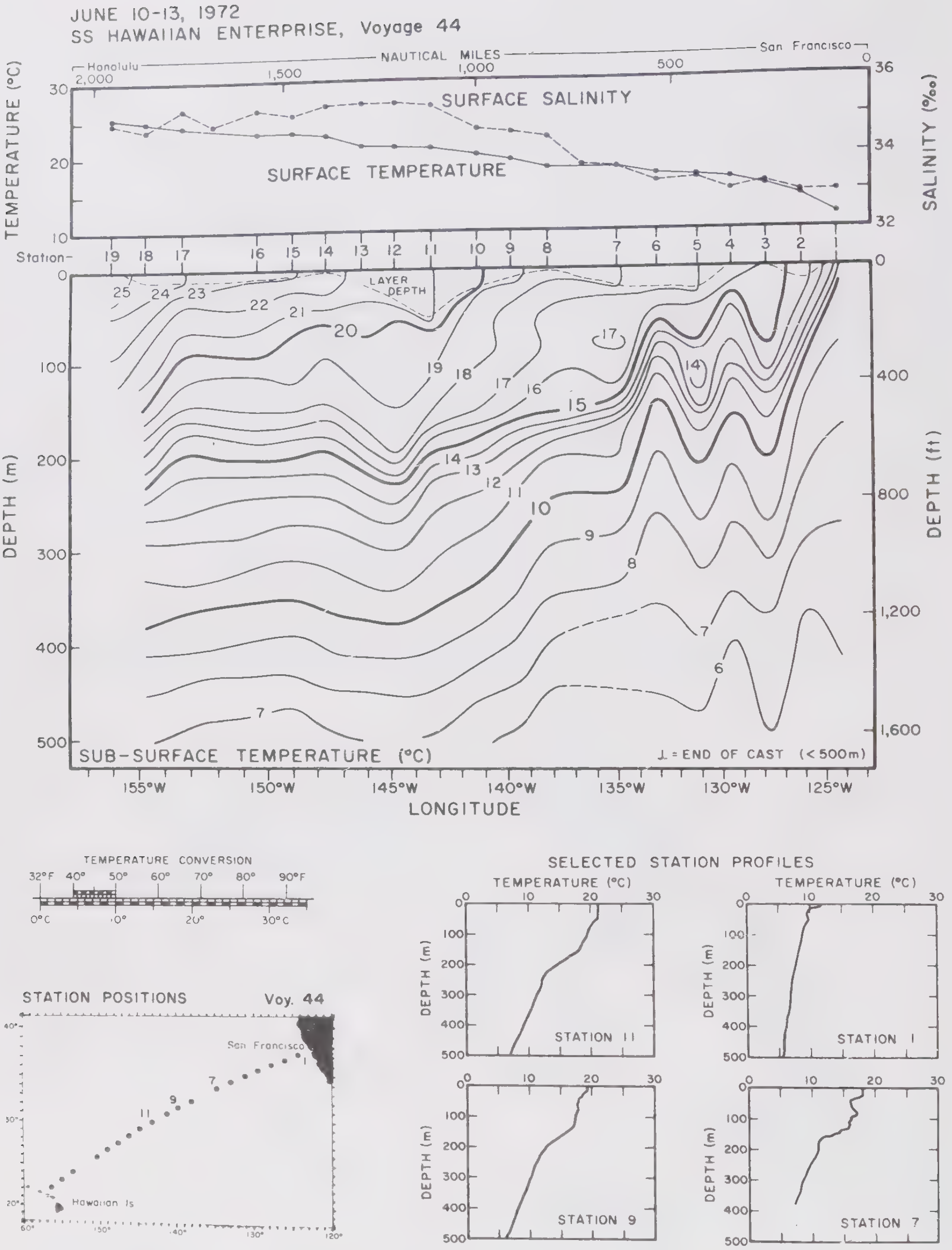

Figure 7.--Vertical thermal structure and surface temperature and salinity between San Francisco and Honolulu. Outer boundary of California current indicated by downward slope of isotherms and increase of salinity at about 135° W (from National Marine Fisheries Service).

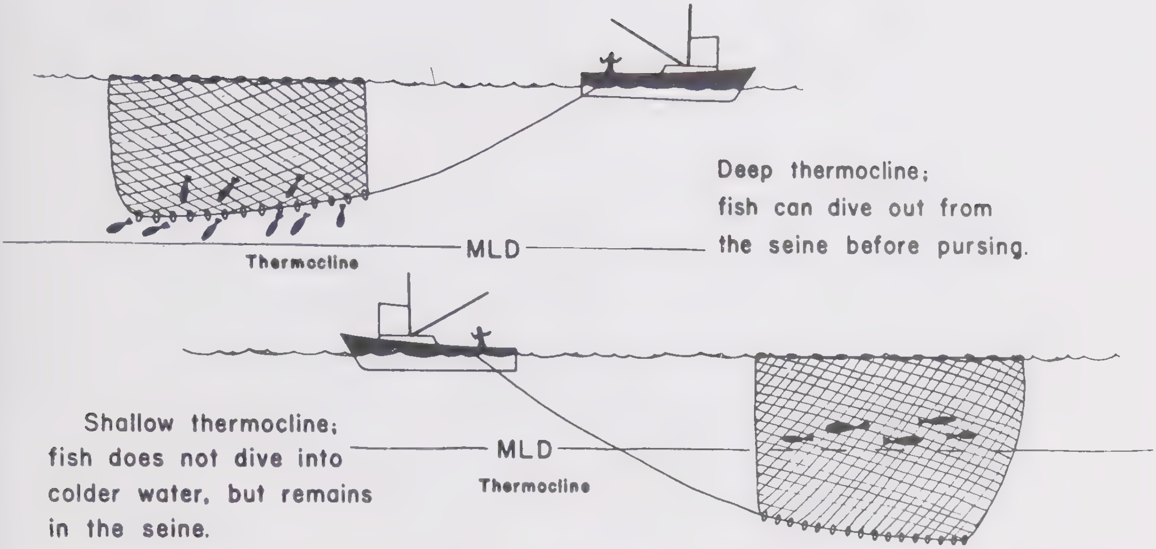
Deep thermocline;
fish can dive out from
the seine before pursing.
MLD
Thermocline
Shallow thermocline;
fish does not dive into
colder water, but remains
in the seine.
MLD
Thermocline

Figure 8.--Schematic example of the effect of different mixed layer depth on purse seining for pelagic fish (from Laevastu and Hela, 1970).

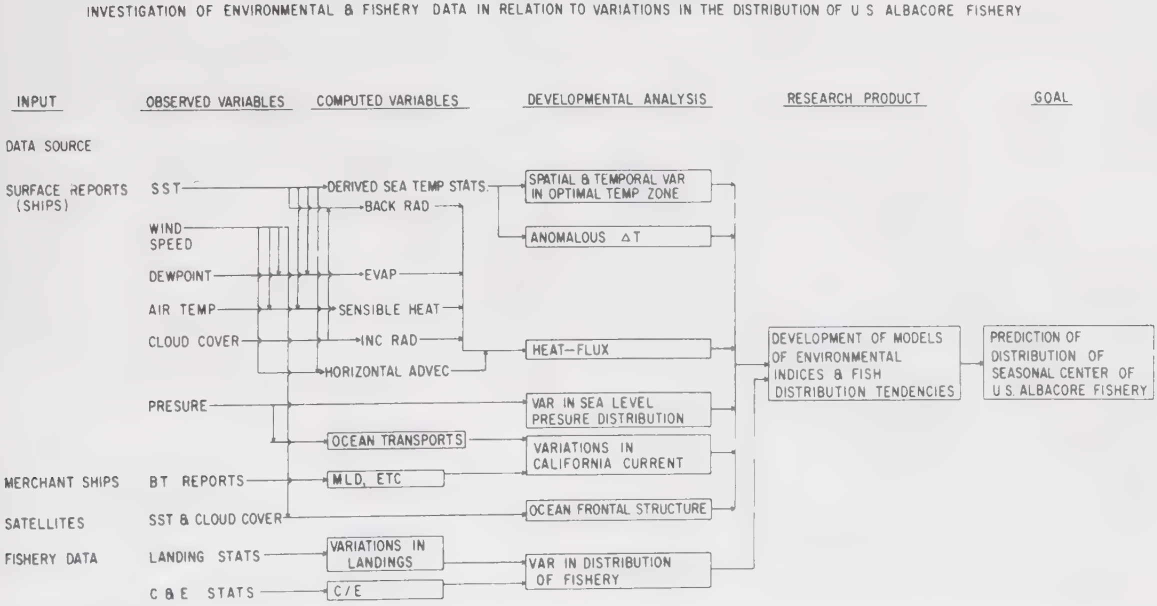
INVESTIGATION OF ENVIRONMENTAL & FISHERY DATA IN RELATION TO VARIATIONS IN THE DISTRIBUTION OF U S ALBACORE FISHERY
INPUT
OBSERVED VARIABLES
COMPUTED VARIABLES
DEVELOPMENTAL ANALYSIS
RESEARCH PRODUCT
GOAL
DATA SOURCE
SURFACE REPORTS (SHIPS)
SST
WIND SPEED
DEWPOINT
AIR TEMP
CLOUD COVER
PRESURE
MERCHANT SHIPS
BT REPORTS
SATELLITES
SST & CLOUD COVER
FISHERY DATA
LANDING STATS
C & E STATS
DERIVED SEA TEMP STATS
BACK RAD
EVAP
SENSIBLE HEAT
INC RAD
HORIZONTAL ADVEC
OCEAN TRANSPORTS
MLD, ETC
VARIATIONS IN LANDINGS
C/E
SPATIAL & TEMPORAL VAR IN OPTIMAL TEMP ZONE
ANOMALOUS ΔT
HEAT—FLUX
VAR IN SEA LEVEL PRESURE DISTRIBUTION
VARIATIONS IN CALIFORNIA CURRENT
OCEAN FRONTAL STRUCTURE
VAR IN DISTRIBUTION OF FISHERY
DEVELOPMENT OF MODELS OF ENVIRONMENTAL INDICES & FISH DISTRIBUTION TENDENCIES
PREDICTION OF DISTRIBUTION OF SEASONAL CENTER OF U.S. ALBACORE FISHERY

Figure 9.--Example of how meteorological, oceanographic, and fishery data are being used to examine the interrelations between environmental conditions and the distribution of albacore tuna in the northeast Pacific (from National Marine Fisheries Service).

7320

APPARENT GROWTH OF YELLOWFIN TUNA FROM THE EASTERN ATLANTIC OCEAN

J. C. LE GUEN[1,2] AND GARY T. SAKAGAWA[1,3]

ABSTRACT

Apparent growth of yellowfin tuna from the eastern Atlantic Ocean was estimated from modal progression of length-frequency distributions by two methods. One was to use fish of unknown age, which gave estimates of parameters of the von Bertalanffy growth function of $L_\infty = 194.8$ cm and $K = 0.035$, on a monthly basis. The other was to use fish of apparent known age, which resulted in $L_\infty = 175.2$ cm and $K = 0.044$. Although the parameter estimates were different, estimates of length at ages 1.5-4.5 years were quite similar with both approaches.

A comparison of growth estimates of yellowfin tuna was made. Estimates from analysis of length-frequency distributions appeared to be superior to those from analysis of scales because they were based on a larger range of fish sizes. However, observed lengths at ages 1.5-5 years were similar for both types of analysis and for yellowfin tuna from both the Atlantic and Pacific Oceans.

It is recommended that observed sizes at age rather than the estimated sizes at age from the von Bertalanffy function be used in estimating yield per recruitment of yellowfin tuna.

There have been several studies (e.g., Le Guen, Baudin-Laurencin, and Champagnat, 1969; Yang, Nose, and Hiyama, 1969) on growth of Atlantic yellowfin tuna (*Thunnus albacares*) but little agreement among them. The disagreement can be traced to at least three sources: first, the kinds of data, e.g., length-frequency distributions and scale readings have been different; second, the method of fitting the von Bertalanffy growth function has varied; and third, the range of fish sizes employed has been different. Because an accurate estimate of growth is important for estimating yield per recruitment by the Beverton and Holt approach (Schaefer and Beverton, 1963), one method that can provide information for rational management of the resource, a study was initiated to estimate growth from the best series of data available and, hopefully, to resolve the disagreement. In this report the results of that study on apparent growth of yellowfin tuna from modal progression of length-frequency distributions are presented and compared to growth estimates derived from published data and computed by standardized procedures.

PLAN OF ANALYSIS

Length frequency samples from commercial landings were employed in our study (Table 1). The fish were caught off Africa by baitboats and purse seiners and were sampled by French and Inter-American Tropical Tuna Commission (IATTC) scientists. (Scientists of the IATTC sampled the Atlantic tuna catch of U.S. vessels under a contract from the National Marine Fisheries Service.) The French scientists sampled the French catches, which were from three general regions—Abidjan, Ivory Coast; Dakar, Senegal; and Pointe-Noire, Congo—and the IATTC scientists sampled the American catches, which were from primarily the Gulf of Guinea. The IATTC samples were caught in both the Abidjan and Pointe-Noire regions, but because

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[1] Alphabetical authorship since the paper is based on independent studies of both authors.

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TABLE 1.—Sources of length data of Atlantic yellowfin tuna caught in the surface fishery off Africa.

Region	Year	Type of length measurement	Type of vessel sampled			Source
			Bait-boat	Small seiner[1]	Large seiner[2]	
Abidjan	1966	Predorsal		X		O.R.S.T.O.M., 1971
	1966-69	Predorsal	X	X		O.R.S.T.O.M., 1971
	1970	Predorsal	X	X	X	O.R.S.T.O.M., 1971
Dakar	1968	Fork	X			Champagnat and Lhomme, 1970
	1969	Predorsal	X	X		Champagnat and Lhomme, 1970
	1970	Predorsal	X	X	X	O.R.S.T.O.M., 1971
Gulf of Guinea	1968-70	Fork			X	Staff, Tuna Population Dynamics Project, 1971[3]
Pointe-Noire	1965-66	Predorsal	X	X		O.R.S.T.O.M., 1971
	1967-68	Predorsal	X	X		Le Guen et al., 1969
	1969	Predorsal	X	X		O.R.S.T.O.M., 1971
	1970	Predorsal	X	X		O.R.S.T.O.M., 1971
	1971	Predorsal	X	X		Unpublished data (Le Guen)

[1] Small purse seiner = less than 500 metric tons capacity.
[2] Large purse seiner = larger than 500 metric tons capacity.
[3] Staff, Tuna Population Dynamics Project. 1971. Size composition of the yellowfin and skipjack tuna purse seine fishery off the west coast of Africa 1968-1970. Unpublished manuscript, 28 p. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

they could not be separated as such, they were treated separately from the French data.

Two methods were employed in our analysis. One approach ("age unknown") was based on all samples from the four regions, for years 1965-70 and with age of size groups unknown. The second approach ("apparent age known") was slightly different. Only fish that were caught in an area from São Tomé to southern Angola, 1967-71, and with the apparent age of each size group known, were employed.

Growth was estimated with the von Bertalanffy growth function. This function is often expressed as,

$$L_t = L_\infty \,[1 - \exp - K\,(t - t_0)],$$

where L_t = length at age t, L_∞ = asymptotic length, K = growth rate, and t_0 = theoretical age when $L_t = 0$. It is fitted to growth data by various procedures (e.g., Walford, 1946; Abramson, 1963; Ricklefs, 1967; Gulland, 1969; Knight, 1969), most of them require data on size at known age. A least-squares procedure that does not contain this limitation was described by Fabens (1965). He fitted a von Bertalanffy function of the form

$$L_{t+\Delta} = L_t + (L_\infty - L_t)\;(1 - \exp - K)$$

to tag-return data, but his procedure is equally applicable to length observations of untagged fish made at t and again at a later date, $t + \Delta$, when the age of the fish is unknown. For tuna, Rothschild (1967) and Joseph and Calkins (1969) employed Fabens' procedure to estimate growth of skipjack tuna (*Katsuwonus pelamis*) from tagging data. We used the Fabens' procedure with monthly mean lengths for individual year classes to estimate growth of yellowfin tuna of unknown age. A computer program written by Tomlinson (Abramson, 1971) was employed to estimate L_∞ in centimeters and K, expressed on a monthly basis. For growth estimates based on apparent known age fish, we used a computer program written by Abramson (1963) and modified by Psaropulos (1966) of a least-squares procedure described by Tomlinson and Abramson (1961).

ANALYSIS WITH UNKNOWN AGE FISH

METHODS

Fish landed at Abidjan, Dakar, and Pointe-Noire (Figure 1) were measured for predorsal length (tip of snout to anterior base of the dorsal fin) by French scientists; fish were measured for fork length by IATTC scientists. In order to standardize the length measurements, we em-

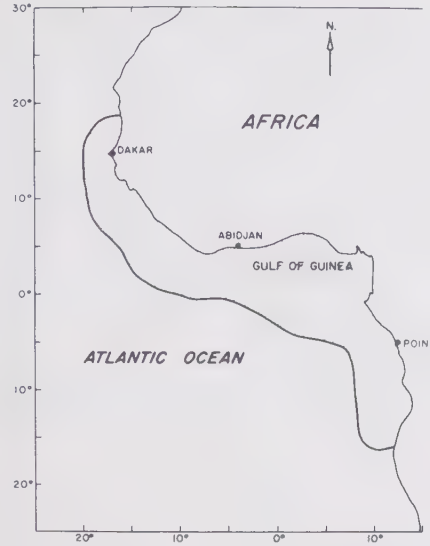

FIGURE 1.—Area off Africa where the surface fishery for yellowfin tuna operates.

ployed the relation, $\log L_f = 0.273 + 1.175 \log L_d$ to convert samples with predorsal length in centimeters (L_d) to fork length in centimeters (L_f). This relation is based on 508 observations and differs from $L_f = (3.624 + 0.212\ L_d)^2$, which was employed by Poinsard (1969). It has a slightly better correlation coefficient ($r = 0.9943$) than Poinsard's equation ($r = 0.9940$) (Lenarz, 1971).[4] Calculated fork lengths based on either equation are accurate only to 1-4 cm.

Monthly length-frequency distributions were tabulated by 4-cm-fork-length groups for samples from each region. Modes were identified and assumed to represent age classes within which lengths were normally distributed. Normal distributions were then fitted to the length frequencies of samples in which two or more modes were present, and the mean length of each age class was estimated (Table 2). A computer program for separating size classes in a mixture that was written and described by Hasselblad (1966) and modified by Tomlinson (1970)[5] was used to separate the age classes and estimate the mean lengths. For samples with only one prominent mode, the modal length, or midpoint of length interval of maximum frequency was considered the "mean length." Representative length-frequency distributions are shown in Figure 2.

Mean lengths for each sample are plotted in Figures 3-6. For each region a serial succession of increasing mean lengths with time was designated a year class, with only one recruited per year although two groups appear to be recruited

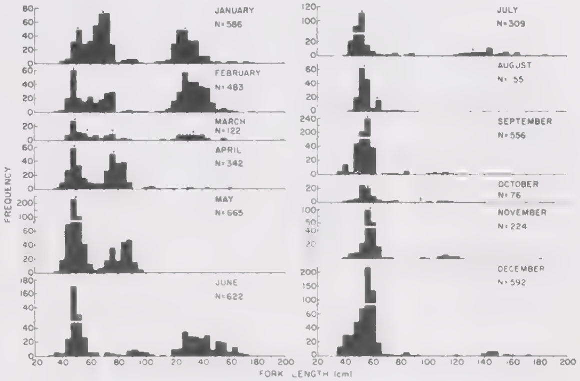

FIGURE 2.—Length-frequency distributions of samples from Pointe-Noire, 1970. Arrows indicate mean lengths of modal groups that were identified by curve fitting.

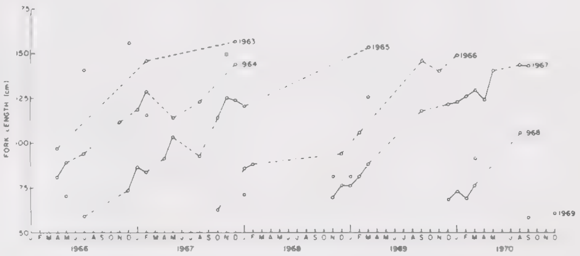

FIGURE 3.—Mean length of size groups of yellowfin tuna as a function of sampling date at Abidjan. Growth of the 1963-69 year classes are indicated

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[4] Lenarz, W. H. 1971. Length-weight relations for five Atlantic scombrids. Unpublished manuscript, 9 p. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, La Jolla, CA 92037.

[5] Tomlinson, P. K. 1970. Program for separating mixture of normal distributions. Unpublished manuscript, 2 p. California Department of Fish and Game, Operations Research Branch, Long Beach, CA 90802.

TABLE 2.—Mean lengths (cm) of modal groups identified in samples from Abidjan, Dakar, Gulf of Guinea, and Pointe-Noire. Values that were not used in the analysis of growth are shown in parentheses.

Region	Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Abidjan	1966				80.7 97.2	(56.8) (70.8) 89.4		59.2 94.2 (140.9)				112.0	73.5 (155.2)
	1967	87.3 118.2	84.3 (115.4) 129.7 146.6		92.0	(48.5) 103.8 114.9			92.8 122.9	(56.0)	62.9 114.8	65.3 125.3 149.7	124.6 144.5 156.8
	1968	(71.7) 86.2 121.9	88.0									69.4 82.3	76.3 94.8
	1969	76.2 (82.3)	81.9 105.4	87.9 112.2 (125.5) 153.6						118.2 145.6		140.0	(50.1) 67.9 122.4
	1970	(54.8) 73.8 123.0 148.4	69.5 125.3	76.9 (92.1) 129.4	124.0	140.0			(55.6) 105.6 143.7	58.1 143.0		(48.0) (58.4)	(43.1) 60.6
Dakar	1968	(44.0)	(56.3) 117.9	(61.2) 122.3	(63.5) 120.7	72.0	(55.3) 70.1 (118.6)	76.0	(63.0) 81.2	(58.4) 88.4	62.3 89.6	66.9 100.1	64.0
	1969	(70.1) 79.4 102.3	75.3 102.6	75.5 105.0	79.9 113.9	(43.6) (57.4) 85.4 112.2	(49.0) (60.1) 93.7	(49.1) 90.9 107.8	(64.8) 95.7 108.2	(69.4) 102.5 118.5	62.4 (75.7) 123.8	53.2 (78.5) 124.5	(61.9) 74.0 119.9
	1970	64.8 124.8	(49.6) 71.8 (88.9) 126.0	(49.4) 73.5 (101.7) 124.3 145.1	(51.4) 72.5 (106.0) 126.4 147.2	(50.6) 76.2 132.4	(53.4) (70.5)	(55.3) (72.3)	(56.3) (74.3) 90.6 133.7	(39.7) (56.4) 92.4	(42.9) 59.2 (72.3) 100.8 145.2	(30.9) (45.0) 63.0 108.8 146.3	(46.4) (57.4) 69.9
Gulf of Guinea	1968								62.9 136.0 (160.2)	57.8 77.0 135.8	70.0 84.4		
	1969								56.8 112.7 124.7	(52.6) 120.3 132.6 151.3	(59.4) 121.5 153.4	156.0	
	1970						(54.8) 87.1 141.2	(55.5) 82.6 (106.8) 143.3 165.7	(56.0)	66.8 140.6	65.6 (103.9)		
Pointe-Noire	1965							(57.7) (78.1) 113.0	(57.4) (80.2) 116.4	59.1 104.0	60.3 (78.4) 121.1	60.0	
	1966									(64.0) 99.1 145.3		63.0 102.2	
	1967			(50.5) 86.9		(52.9) 90.6 113.8 155.9	(58.0) 88.8	(53.4) 102.1	(53.6) 104.0 113.0	(59.3) 105.1	(61.4) 108.4	112.0	(68.0)
	1968	(60.7) 122.7 (154.6)				(68.0)	(56.4) (73.4) 120.9	59.7 (71.1) (85.4) 134.0 140.0	62.2 (73.6) (90.9) 130.8 152.7	64.6 (75.3) (87.0) 143.8 (156.6)	65.9 (76.2) (91.9) 136.8	(75.0)	72.7 (89.5) (101.5)
	1969	76.0		86.3 (111.1)	49.6 94.3 (117.7) 148.4 164.8	100.0	(56.9) 104.2	(55.7) (112.9) 154.5	(45.8) (56.3) (117.5) 156.0	(57.7) 112.7	(57.4) 114.6	59.9 (127.7)	56.6 127.1
	1970	(51.5) 69.0 129.7	(48.5) 65.5 134.7	(48.8) (57.5) 75.6 134.1	(48.9) 76.8	(49.9) 82.8	(50.7) 131.8	(51.3) 132.2	(53.7) 62.2	(56.0)	(55.3) 93.5	(57.6) 113.5	(56.0)

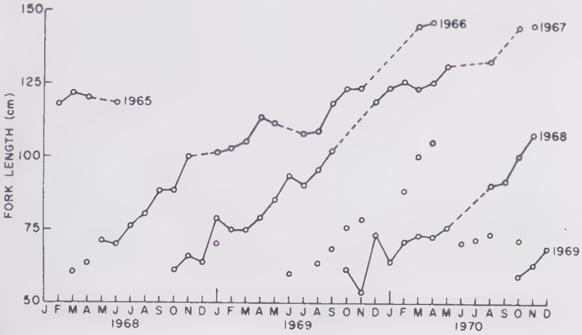

FIGURE 4.—Mean length of size groups of yellowfin tuna as a function of sampling date at Dakar. Growth of the 1965-69 year classes are indicated.

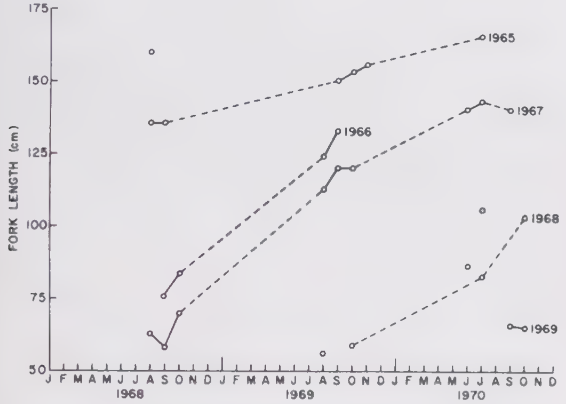

FIGURE 5.—Mean length of size groups of yellowfin tuna from the Gulf of Guinea. Growth of the 1965-69 year classes are indicated.

in some years. Recruitment is assumed to be completed in the second year of life (Le Guen et al., 1969).

RESULTS

Recruitment

Yellowfin tuna are recruited into the surface fishery when about 60 cm long. Recruitment is year-round but most pronounced during June to December. Two groups of yellowfin tuna appear to be recruited in some years. For example, in 1968 at Pointe-Noire (Figure 6) one group entered in January and another in August-September. The January group was of low relative abundance and persisted up to a length of about 90 cm, while the August-September group was of high relative abundance and discernible up to a length of about 140 cm. A similar phenomenon was described by Hennemuth (1961) and later verified by Davidoff (1963) for yellowfin tuna of the eastern Pacific Ocean. Hennemuth suggested that sampling bias, differential growth in a year class, and multiple spawning were some possible causes of the phenomenon. Variation in the seasonal distribution of fishing effort can be added as another possible cause.

Year Class Difference in Apparent Growth

Estimates of apparent growth for individual year classes for each region are shown in Table 3.

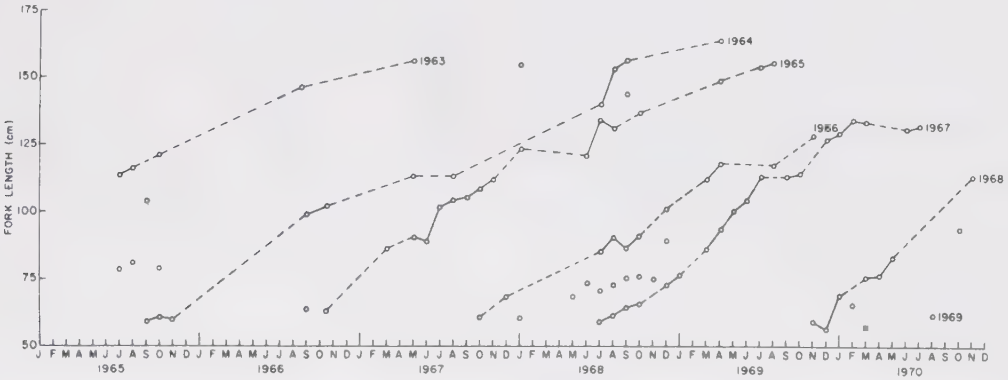

FIGURE 6.—Mean length of size groups of yellowfin tuna as a function of sampling date at Pointe-Noire. Growth of the 1963-69 year classes are indicated.

TABLE 3.—Estimates of parameters of the von Bertalanffy growth function for yellowfin tuna of unknown age from the eastern Atlantic Ocean.

Region	Year class	L_∞	K	No. of observations	Range of lengths (cm)
Abidjan	1963	Linear		2	97.2-156.6
	1964	138.6	0.137	9	80.7-149.7
	1965	275.2	0.016	11	59.2-153.6
	1966	Linear		9	62.9-148.4
	1967	155.1	0.086	13	69.4-143.7
	1968	Linear		4	67.9-105.6
	All years	185.0	0.043	48	59.2-156.6
Dakar	1965	Linear		2	117.9-122.3
	1966	Linear		18	70.1-147.2
	1967	201.5	0.038	20	62.3-146.3
	1968	557.2	0.008	11	53.2-108.8
	All years	307.9	0.017	51	53.2-147.2
Gulf of Guinea	1965	677.4	0.002	5	135.8-165.7
	1966	497.5	0.009	3	77.0-132.6
	1967	174.4	0.052	8	57.8-143.3
	1968	Linear		2	56.8- 87.1
	All years	185.0	0.041	18	56.8-165.7
Pointe-Noire	1963	168.3	0.067	5	104.0-155.9
	1964	273.9	0.017	10	59.1-164.8
	1965	162.9	0.059	16	63.0-156.0
	1966	191.9	0.024	11	61.4-127.7
	1967	160.2	0.051	17	59.7-134.7
	1968	177.8	0.033	8	56.6-113.5
	All years	210.1	0.027	67	56.6-164.8
All regions	1963	158.5	0.136	7	97.2-156.6
	1964	237.4	0.023	19	59.1-164.8
	1965	191.0	0.034	34	59.2-165.7
	1966	895.7	0.003	41	61.4-148.4
	1967	172.6	0.054	58	57.8-146.3
	1968	502.4	0.009	25	53.2-113.5
	All years	194.8	0.035	184	53.2-165.7

In some instances, the estimates of K and L_∞ are unexpectedly too high or too low, indicating that the estimates are inappropriate for the entire life span of the species. According to Knight (1968) and Le Guen (1971), a possible cause of variation in K and L_∞ is lack of size measurements for the entire life span of the species. This appears to be the case in some instances for our data. Length measurements for Dakar, for example, were from catches made predominantly by pole-and-line, or baitboats that generally catch small fish, a characteristic that is well documented (Pianet and Le Hir, 1971). Consequently, large fish were underrepresented in the samples, resulting in heavier weight on the lower size groups. Estimates of L_∞ were therefore unreasonably high, while those of K were unreasonably low. It should be noted that generally L_∞ and K are inversely correlated (Beverton and Holt, 1959).

For some year classes, apparent growth appears to be exceptionally faster than for others. Apparent growth of yellowfin tuna from Pointe-Noire can best illustrate this point (Figure 6). The 1965 and 1967 year classes grew at a faster rate than the 1964 or 1966 year class. The result was an apparent convergence of the growth curve for the 1964 year class with that for the 1965 year class, and the 1966 year class with the 1967 year class. In each case, there appears to be no relation between the time of recruitment and the rate of growth.

Regional Differences in Apparent Growth

For each region, the von Bertalanffy equation was fitted to data for all year classes combined. Apparent growth of yellowfin tuna from Abidjan, Gulf of Guinea, and Pointe-Noire was quite similar for sizes (ranged from about 60 to 160 cm long) observed in the samples (Figure 7). Apparent growth of Dakar fish, on the other hand, seemed exceptionally faster, which is at-

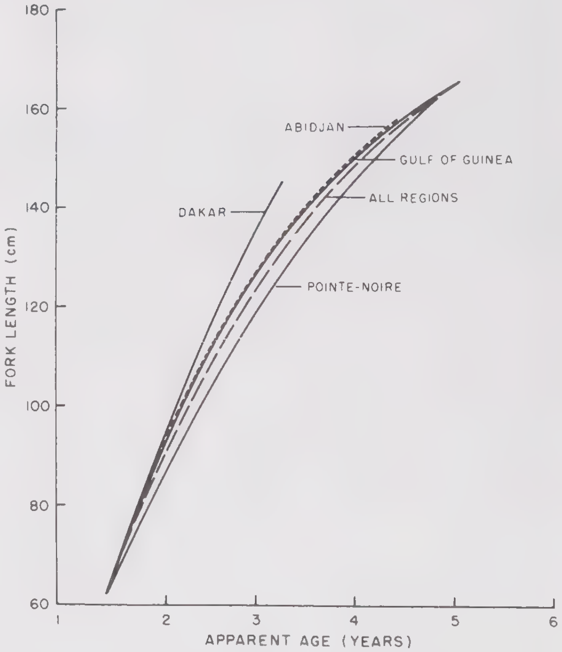

FIGURE 7.—Growth of yellowfin tuna from the eastern Atlantic Ocean.

tributed to lack of data on older fish as was discussed earlier. The range of mean length is 50 to 150 cm.

Estimated Length at Age

An estimate of $L_\infty = 194.8$ cm, and $K = 0.035$, on a monthly basis, was derived from data for all year classes and regions combined (Table 3). We believe these estimates are the "best," on the average, for yellowfin tuna of the eastern Atlantic Ocean, because they were based on data from a broad geographic area off Africa and a wide range of sizes. The estimated growth curve is quite similar to that for Abidjan, Gulf of Guinea, and Pointe-Noire (Figure 7). For individual year classes, however, estimates of L_∞ and K can be expected to deviate from the average, since there is an apparent difference in apparent growth among year classes (Table 3) and considerable scatter of observed mean lengths around the average curve (Figure 8).

Data on growth of tagged yellowfin tuna in the eastern Pacific and on the time of spawning in the Atlantic were used to estimate t_0 in months. The above best estimates of parameters of the von Bertalanffy equation were then used to estimate the length of yellowfin tuna at particular ages. A tacit assumption of this method of estimating length at age is that the von Bertalanffy function is a valid growth model for yellowfin tuna, and the date of birth is constant.

Schaefer, Chatwin, and Broadhead (1961) reported that yellowfin tuna of 40-49 cm long at tagging grew at a rate of 33 cm/year. They indicated that growth was probably adversely affected by tagging, implying that their estimate was too low.

Le Guen et al. (1969) reviewed the literature on time of spawning of yellowfin tuna in the Atlantic Ocean. They concluded that spawning occurred primarily at temperatures greater than 26°C and salinity of about 33.5‰. From seasonal distributions of temperature, salinity, and tuna larvae captured off Africa, they estimated that spawning peaked on about March 1 off Pointe-Noire and on about July 1 off Dakar.

From the above information together with the fact that recruitment into the surface fishery is generally from June to December, we estimated that yellowfin tuna were, on the average, 18 months old at recruitment, about 60 cm long, and $t_0 = 7.48$. Estimates of length at age were calculated with $L_\infty = 194.8$, $K = 0.035$, and $t_0 = 7.48$, employed in the von Bertalanffy function (Table 4). The estimates are graphed in Figure 8, together with monthly mean lengths of individual year classes of each region. There is considerable scatter of the data about the line and an indication that lengths at age 50 months and older are overestimated.

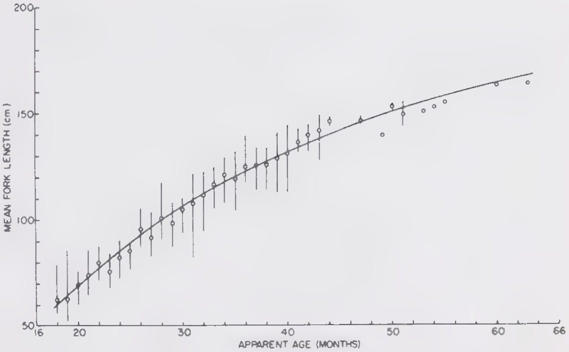

FIGURE 8.—Mean length of year classes of yellowfin tuna as a function of age. The curve is for all year classes and regions combined and is estimated by a von Bertalanffy growth function. Average of observed mean lengths (circles) and the range of mean lengths (vertical line) at various estimated ages are shown.

Estimated Weight at Age

Length can be converted to weight with a weight-length relation. Lenarz (see footnote 4) reported that the weight-length relation for yellowfin tuna from the eastern Atlantic is $W = 0.0000214\ L_f^{2.9736}$, where W = weight in kilograms and L_f = fork length in centimeters. This equation was employed to convert estimates of length at age to weight at age (Table 4).

ANALYSIS WITH APPARENT KNOWN AGE FISH

METHODS

The method of analysis with apparent known

TABLE 4.—Observed and estimated size at various ages of yellowfin tuna from the Atlantic and Pacific Oceans. Length (cm) is shown for most ages, and weight (kg) in parentheses for a few ages. Estimated length is based on the von Bertalanffy growth function.

Age (years)	Source of data											
	Yang et al., 1969		Le Guen et al., 1969				Present study				Davidoff, 1963	
	Atlantic Ocean		Eastern Atlantic				Eastern Atlantic				Eastern Pacific	
			Pointe-Noire		All regions		São Tomé-Angola		All regions			
	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated	Observed	Estimated
1.0	--	54.0	--	33.2	--	32.2	--	17.3 (0.1)	--	28.5 (0.4)	--	34.6
1.5	66.1	75.8	64.6	62.9	63.8	60.0	61.5	53.9 (3.0)	62.2	60.0 (4.2)	--	61.9
2.0	86.1	94.9	84.6	86.6	79.5	83.1	77.6	82.0(10.5)	82.3	85.5(11.9)	83.0	84.7
2.5	104.1	111.5	108.3	105.6	103.9	102.0	111.0	103.6(21.1)	105.0	106.2(22.7)	105.0	103.8
3.0	120.0	125.9	--	120.9	124.0	117.7	116.1	120.2(32.8)	125.0	123.0(35.1)	122.0	119.7
3.5	132.9	138.5	132.2	133.1	132.2	130.6	132.2	133.0(44.3)	140.6	136.6(48.0)	136.0	132.9
4.0	--	149.4	--	142.9	--	141.3	135.6	142.8(54.7)	--	147.6(60.5)	141.0	144.0
4.5	--	158.9	147.0	150.7	143.6	150.1	147.0	150.3(63.8)	153.4	156.6(72.0)	--	153.3
5.0	--	167.2	152.0	157.0	152.0	157.4	153.7	156.1(71.3)	164.8	163.8(82.4)	--	161.0

age fish were similar to those described by Le Guen et al. (1969) and are briefly described as follows. Predorsal length-frequency distributions were tabulated for monthly samples collected in 1967-71 off Pointe-Noire in an area from São Tomé to southern Angola. Modes were selected by comparison of successive maxima in the length-frequency distributions and mean predorsal length estimated for each size group by a method described by Gheno and Le Guen (1968). Mean dorsal lengths were then converted to fork lengths with the aid of Table 5, which was based on fish measured for both predorsal and fork lengths at Pointe-Noire. The data in Table 5 give a fork length-predorsal length relation of log $L_f = 0.299 + 1.162 \log L_d$ that is not significantly different from the equation used earlier.

An estimated age was assigned to each size group (Table 6) based on: (1) date of birth of yellowfin tuna caught off Point-Noire is on the average March 1 and (2) recruitment occurs in the second year of life (Le Guen et al,. 1969). Estimates of parameters of the von Bertalanffy function were then calculated with Psaropolos' (1966) computer program.

Length at age estimates were converted to weight at age with the weight-length relation of Lenarz (see footnote 4), which was mentioned earlier.

TABLE 5.—Predorsal length and fork length measurements of yellowfin tuna landed at Pointe-Noire, 1967-71.

Predorsal length (cm)	Mean fork length (cm)	Number of obser-vations	Predorsal length (cm)	Mean fork length (cm)	Number of obser-vations
12	39.0	11	31	109.5	46
13	40.9	21	32	111.3	33
14	45.0	18	33	116.1	27
15	47.3	37	34	118.8	19
16	50.0	36	35	122.9	26
17	53.9	33	36	132.3	24
18	57.2	58	37	134.7	35
19	59.8	83	38	138.4	25
20	63.1	66	39	143.7	28
21	66.3	43	40	145.7	29
22	71.0	20	41	149.7	29
23	74.6	23	42	152.3	14
24	76.0	18	43	158.8	5
25	81.1	16	44	164.0	5
26	84.2	16	45	166.3	10
27	89.0	9	46	172.0	6
28	92.8	21	47	175.4	8
29	99.1	28	48	177.8	7
30	104.9	27	49	179.8	2

RESULTS

Estimates of parameters of the von Bertalanffy function were $L_\infty = 175.17$ cm (SE $= 3.67$), $K = 0.044$ per month (SE $= 0.003$), and $t_0 = 9.643$ months (SE $= 0.815$). These estimates are quite similar to those derived by Le Guen et al. (1969) for the Pointe-Noire region based on only data from 1967-68 (Table 7); but L_∞ is significantly lower and K significantly higher than our best estimates for yellowfin tuna from a larger area of the eastern Atlantic, even when the difference in range of lengths in the data is taken into account. On the other hand, length at age and weight at age estimates for ages 1-5 years are quite similar to those for the entire eastern Atlantic (Table 4). Thus, we conclude

TABLE 6.—Size classes (cm) of yellowfin tuna identified in samples from São Tomé to southern Angola. Year classes are separated by horizontal lines.

Age (months)	1967-68[1]	1969	1970	1971
18	64.5		58.5	
19			59.8	
20			61.4	
21	70.3			
22	85.0	75.3	68.6	58.5
23	85.1		71.0	63.1
24	84.6	82.6	74.6	68.6
25	89.0	90.9	81.1	72.8
26	90.6	104.9	82.6	74.6
27	91.0	107.2	92.8	76.0
28	95.5	107.2		86.6
29	102.6			
30	108.3	113.7		
31	107.7	116.1		
32	109.4	127.5		
33	114.5	127.5		
34	124.0			
35	120.0	111.3		
36		116.1		
37	122.0	118.8		
38	126.7			
39	123.5			
40	134.7			
41	136.8			
42	132.2			
43	139.0			
46			133.5	
47	138.6			
48			136.5	134.7
52	147.0		141.0	138.4
53	151.3		143.7	
54	147.0			
55	150.5			
60	152.0			155.5
61		149.7		156.0
64				158.8
65	163.4			160.0
66	161.9			
73		166.3		
74		168.1		
75		168.0		170.1
76				170.1
77				170.1

[1] Data from Le Guen et al. (1969).

that there is no appreciable difference in the estimate of apparent growth of yellowfin tuna from the region of the eastern Atlantic, illustrated in Figure 1 or from a smaller region within that part such as off Pointe-Noire.

COMPARISON OE GROWTH ESTIMATES

Studies on growth of yellowfin tuna have largely been based on two types of data: length-frequency distributions and scale readings. For comparative purposes we chose two studies that were based on scale readings—one each from the Pacific (Yabuta, Yukinawa, and Warashina, 1960) and Atlantic (Yang et al., 1969)—and three studies that were based on modal progression of length-frequency distributions—two from the Pacific (Davidoff, 1963; Moore, 1951) and one from the Atlantic (Le Guen et al., 1969)—for comparison with our best estimates for the eastern Atlantic. The procedure of estimating the parameters of the von Bertalanffy function was standardized with the use of the Fabens' (1965) procedure whenever appropriate data were available.

ESTIMATES FROM SCALE READINGS

Lengths at mark formation from interpretation of marks on scales were reported by Yabuta et al. (1960). They indicated that mark formation occurs twice a year, in March-April and in September-October, or 6 months apart in the western Pacific. An estimate of growth was calculated from their data with 6 months between marks (Table 7). Growth appears to be substantially slower in the western Pacific than in the eastern Atlantic (Figure 9). Either growth is indeed slower in the western Pacific or the interpretation of scale marks by Yabuta et al. is in error. The latter possibility is suggested by the absence in their data of fish greater than 119 cm long with a designated mark, although fish as large as 161 cm long were reportedly sampled. Moreover, only about 42% of their scales were readable. Other studies made in the western Pacific (see Shomura, 1966; Suzuki, 1971) suggest that growth was underestimated by Yabuta et al.

$L_\infty = 222.8$ cm and $K = 0.023$, on a monthly basis, were estimated by Yang et al. (1969). Their estimates were based on scale readings of 296 yellowfin tuna caught by the Atlantic longline fishery. Since Yang et al. used the Walford (1946) procedure to estimate growth, we recalculated growth with the Fabens' procedure using the data of Yang et al. and the assumption that the scale marks formed every 6 months. The results (Table 7) were not markedly different from the estimates by Yang et al. Compared to our best estimate of growth rate (K), on the other hand, their estimate is substantially

TABLE 7.—Estimates of parameters of the von Bertalanffy growth function for yellowfin tuna from the Atlantic and Pacific Oceans. Estimates are based on data reported in various studies, and were calculated by Fabens' (1965) procedure, except those of Le Guen et al. (1969).

Region	L_∞	K	Range of length (cm)	Source of data	Data
Atlantic Ocean	223.0	0.023	66-133	Yang et al., 1969	Scale readings; Table 6
Eastern Atlantic				Le Guen et al., 1969	Length frequencies; estimates reported by authors
Dakar	206.6	0.026	63-162		
Pointe-Noire	182.4	0.037	64-162		
All areas	191.7	0.032	63-162		
Eastern Atlantic				Present study	Length frequencies (Age unknown)
Abidjan	185.0	0.043	59-157		
Dakar	307.9	0.017	53-147		
Gulf of Guinea	185.0	0.041	57-166		
Pointe-Noire	210.1	0.027	57-165		
All areas	194.8	0.035	53-166		
Eastern Atlantic São Tomé-Angola	175.2	0.044	58-170	Present study	Length frequencies (Age known)
Central Pacific	191.9	0.036	47-168	Moore, 1951	Length frequencies; Table H
Eastern Pacific	200.3	0.030	69-148	Davidoff, 1963	Length frequencies; Table 6
Western Pacific				Yabuta et al., 1960	Scale readings; Table 5
Males	202.1	0.023	58-119		
Females	174.9	0.031	57-119		
All sexes[1]	188.4	0.027	57-119		

[1] Estimates were based on weighed average length for each scale mark reported by Yabuta et al. (1960). Sample size of each sex was used as the weighing factor.

smaller. Possibly this smaller K is caused by error in the interpretation of scale marks and the paucity of large fish in their data. The maximum number of marks observed by Yang et al. was five, with a corresponding mean length of 132.9 cm at time of fifth mark formation, but fish as large as 180 cm long were reportedly sampled. For our study, fish as large as mean length 166 cm were used in the calculations.

ESTIMATES FROM MODAL PROGRESSION

Davidoff (1963) examined modal progressions of length-frequency distributions of eastern Pacific yellowfin tuna caught by baitboats and purse seiners and calculated with the Walford procedure $L_\infty = 167$ cm and $K = 0.05$, on a monthly basis, which he noted were similar to earlier estimates reported by Hennemuth (1961). Davidoff's estimates were based on average modal length at each age of all year classes combined. Equal weight was therefore given to each datum point in his calculation.

Using the Fabens' procedure and data for each year class reported by Davidoff (his Table 6), we recalculated the growth estimates. The results, $L_\infty = 200.3$ and $K = 0.030$, are considerably larger for L_∞ and smaller for K than Davidoff's estimates but similar to our estimates for Atlantic yellowfin tuna (Table 7).

Hennemuth (1961) reported that fish 70 cm long in the eastern Pacific were about 20 months old. Entered into the von Bertalanffy equation, this gives a t_0 of 5.67 months with $L_\infty = 200.3$ and $K = 0.030$, and a means of estimating length at age for eastern Pacific yellowfin tuna. The results are shown in Table 4. They compared favorably with our estimates for Atlantic yellowfin tuna, although apparent growth in the eastern Atlantic is 0.9 to 2.8% faster than that in the eastern Pacific for ages 2 through 5 years.

Moore (1951) based his estimates of growth on length-frequency distributions of yellowfin tuna caught primarily by longline gear in the central Pacific. He used the Walford procedure and calculated $L_\infty = 190.0$ cm and $K = 0.037$ per month. Because of a limitation of Walford's

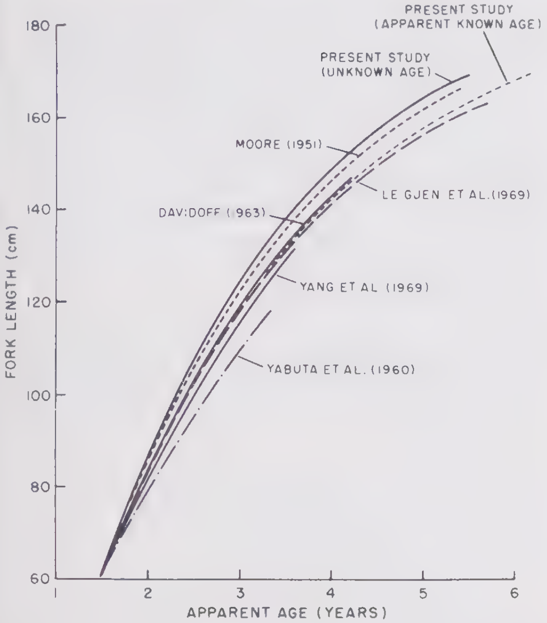

FIGURE 9.—Comparison of growth of yellowfin tuna from the Pacific and Atlantic Oceans. Curves were adjusted to a common base of age 1.5 years = 60 cm long and were estimated, except for that of Le Guen et al. (1969), from data reported in various studies.

method—requiring length measurements at equal time intervals—Moore was able to use only 16 out of his 25 observations. We recalculated L_∞ and K, using the Fabens' procedure and the 25 observations reported by Moore (his Table H). The estimates, $L_\infty = 191.9$ and $K = 0.036$, differ slightly from those of Moore and are very similar to our estimates for Atlantic yellowfin tuna.

Le Guen et al. (1969) estimated growth of yellowfin tuna from Dakar, Pointe-Noire, and both regions combined, based on modal progression of length-frequency samples (Table 7). Their samples were identical to some used in our study, but their estimate of growth for combined regions is slightly lower than ours; the difference in estimated lengths for ages 2 through 5 years is 2.8 to 4.3% less (Table 4). Part of the difference is in the method of analysis. The estimates by Le Guen et al. were based on mode selection from predorsal length distributions, and the lengths of size groups were not assumed to be normally distributed. Predorsal lengths were then converted to fork length; whereas in our best estimate predorsal length was converted to fork length by a log function before frequency distributions were analyzed, and the lengths of size groups were assumed to be normally distributed. Furthermore, Le Guen et al. assumed that the date of birth of fish of each year class of a region was the same and accordingly ages were assigned to size classes; such an assumption was not made for our estimate of K and L_∞; but for obtaining t_0 we assumed that yellowfin tuna of 60 cm long are 18 months old. Nevertheless, the difference is insignificant in view of the fact that there is considerable variability in observed mean lengths at age (Figure 7).

DISCUSSION

It is obvious from the results that estimates of growth of yellowfin tuna are quite variable and largely dependent on the method of analysis. Both the length-frequency and scale methods are based on various assumptions that are not always satisfied. For example, the assumption in the length-frequency method that size groups represent age groups, and the age groups are formed once a year, i.e., hatching within a short period, or season, is not completely satisfied for yellowfin tuna, since spawning occurs over several months (Matsumoto, 1966; Le Guen et al., 1969; Richards, 1969). Nevertheless, in many areas, as in the eastern Atlantic, there is generally a peak month of spawning (Le Guen et al., 1969) that can create a size group discernible in size-frequency distributions in later dates.

The scale method assumes that the scale marks are formed at regular intervals. So far, this assumption has not been satisfactorily verified for yellowfin tuna, although Yabuta et al. (1960) and Yang et al. (1969) have indicated that the marks formed every 6 months. Furthermore, because yellowfin tuna generally spawn over an extended season, the age at first annulus formation is not the same for all individuals of a year class. The back-calculated length at age I may therefore be questionable. It is surprising, however, that the observed lengths at age are remarkably similar for studies based on the scale and length-frequency methods (Table 4). This suggests that the marks on scales of Atlantic yellowfin tuna are indeed layed down at regular intervals and that observed lengths at age rather than estimates of parameters of the von Bertalanffy function are more meaningful in comparison of growth of yellowfin tuna. For such a comparison, the average growth rate of Atlantic yellowfin tuna is 17 cm/6 months, based on the scale method, and 18 cm/6 months, based on the length-frequency method for ages 1.5-3.5 years.

The comparison of observed lengths at age also indicates that there is little difference between growth of Atlantic and Pacific yellowfin tuna (Table 4). Yang et al. (1969), on the other hand, suggested that growth is faster in the Atlantic than in the Pacific. We analyzed their data with analysis of covariance and found that their Walford curves for the Atlantic and Pacific yellowfin tuna were not significantly different from a common line ($F_{2,5} = 0.474$) nor from parallel lines ($F_{1,5} = 0.904$). Thus the suggestion by Yang et al. was not demonstrated by their data, but in fact, growth of yellowfin tuna appears to be similar in the two oceans.

Finally, since the parameters of the von Bertalanffy growth function are sensitive to the method of analysis and range of sizes used to estimate them, we recommend that the observed size at age rather than the estimated size at age from the von Bertalanffy growth function be used in estimating yield per recruitment. The Ricker (1958) model of yield per recruitment, for example, is appropriate for observed values.

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732

DEPENDENCE OF CATCH RATES ON SIZE OF FISH LARVAE

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INTRODUCTION

Numerous authors have used data obtained from systematic collections of fish larvae to estimate absolute or relative abundances of fish. Often a density measure of the number of larvae summed over size is used: Ahlstrom (1961) compared the relative abundances of rockfish larvae collected off the coasts of California and Baja California; Ahlstrom (1966) presented an extensive set of data collected in the same area and examined the abundance of Pacific sardine and northern anchovy over a period of 15 years; Ahlstrom (1968) employed the same data to estimate the spawning stocks of Pacific sardine and northern anchovy. Einarsson (1961) compared catches of *Sebastes* larvae from waters off the coast of Iceland over a period of several years; Hansen (1968) estimated year class strengths of cod from larvae data; Raitt (1964) used data obtained from a survey of *Sebastes* larvae off the coast of Scotland to estimate the number of adult females; Smidt (1968) compared yearly catches of larvae of Greenland halibut and halibut.

Although the use of fish larvae summed over size appears to be widespread, possible sources of error, such as avoidance, differential retention by size, behavior, and variable growth and mortality rates need to be evaluated.

Several studies, Ahlstrom (1954), Ahlstrom (1965), Clutter and Anraku (1968), Farris (1961), Isaacs (1965) and Vannucci (1968), have examined these sources of error, but much work is needed before these sources of errors can be eliminated.

Catch curves of larvae of four species of fish, Pacific hake (*Merluccius productus*), Pacific sardine (*Sardinops caeruleus*), northern anchovy (*Engraulis mordax*), and jack mackerel (*Trachurus symmetricus*) are examined in this paper. A simple mathematical expression is derived to describe portions of the catch curve. Variability among years, areas, and species is examined and discussed with respect to the sources of error previously mentioned. The effect of variability in the catch curves on catches of fish larvae summed over size is shown.

The data were obtained from California Cooperative Oceanic Fisheries Investigations surveys of the coastal waters of California and Baja California. These surveys used cylindrical-conical plankton nets constructed of # 30 xxx grit gauze (mesh size 0·5504 mm) with a mouth diameter of 1 m. Oblique hauls to a depth of 140 m, depth permitting, sampled the water column. Each haul sampled about 500 m^3 of water. Counts of fish larvae were standardized to numbers per 10 m^2 of surface area. Ahlstrom (1966) described procedures of sampling in greater detail.

This study utilizes data from about 12 000 samples. Only data taken during the months of January through July were used. Sampling was not adequate for other months, and previous studies showed that the preponderance of larvae of the species of concern is taken during the January-through-July period. Differences in effort per month were adjusted by the use of a weighting factor proportional to the inverse of the effort per month. No attempt was made to adjust for differences in effort per area. Catch curves of jack mackerel and Pacific hake larvae were derived from data obtained during 1966. The study of Pacific sardine and northern anchovy utilizes data from 1951–1960. Pacific hake larvae have only been measured in recent years. Although jack mackerel larvae have been measured since 1951, the data are not readily available. Samples were not taken during the month of March in 1966.

CATCH CURVES

PACIFIC HAKE

Figure 170 illustrates day and night catch curves of Pacific hake larvae collected during 1966. These curves have most of the characteristics of catch curves I have examined for fish larvae. A mode occurs at 2·5 mm for the night catches and at 3 mm for the day catches. A portion of Pacific hake larvae at smaller sizes probably passes through the mesh of the collecting gear causing the modes. The curves then decline in an approximately exponential fashion. There is a slight tendency for the rate of decline to decrease with increasing size. The ratio of night to day catches tends to increase with size. The phenomenon has been attributed to net avoidance by several authors. Insignificant numbers of Pacific hake larvae were captured at sizes greater than 14 mm. Finally there is an indication that catches are higher at whole mm sizes than at the preceding half mm sizes. This may be due to a bias towards measuring individuals as whole units rather than half units.

Since the decline in catch, as size increases, is nearly exponential, I chose to use an exponential equation to describe mathematically the catch curves between the modal size and largest size of significant catches. The catch equation is given by

$$N_{sd} = N_{s_0d}A\exp[-B(s-s_0)]E_{sd} \qquad (1)$$

where N_{sd} = number of larvae of size s caught during time d

$s = s_0, \ldots\ldots, s_t$

s_0 = modal size

s_t = largest size of significant catches

d = time of day; *i.e.*, day (0) or night (1)

A = constant

B = instantaneous rate of decline in catch with size

E_{sd} = error term assumed to be independent of s and d and to have a log-normal distribution.

The parameters in equation (1) change for night and day because of the differences between night and day catch rates. An equation was derived to describe simultaneously the night and day catch curves. The ratio between day and night catches tends to increase in a linear fashion. However, it is simpler to estimate parameters of a model that assumes that the night to day ratio increases in an exponential fashion because the change of catch rate with size is exponential. I believe that the increased simplicity justifies the decrease in precision. The new equation is:

$$N_{sd} = N_{s_0d}A\exp[-B(s-s_0)]\exp[Cd(s-s_0)]E_{sd} \qquad (2)$$

where C = instantaneous rate of increase of the night to day ratio with size.

The parameters A, B, and C were estimated by the technique of multiple linear regression after transforming the equation to

$$\left.\begin{aligned} \log_e(N_{sd}/N_{s_0d}) &= \log_e(A) - B(s-s_0) \\ &\quad + Cd(s-s_0) + \log_e(E_{sd}) \end{aligned}\right\} \quad (3)$$

The results are shown in Table 94. For the Pacific hake, approximately 92% (R^2) of the variance is explained by the model. The estimated value of B is 0·48. This means that the catch rate at night of Pacific hake declines about 38% per mm of growth.

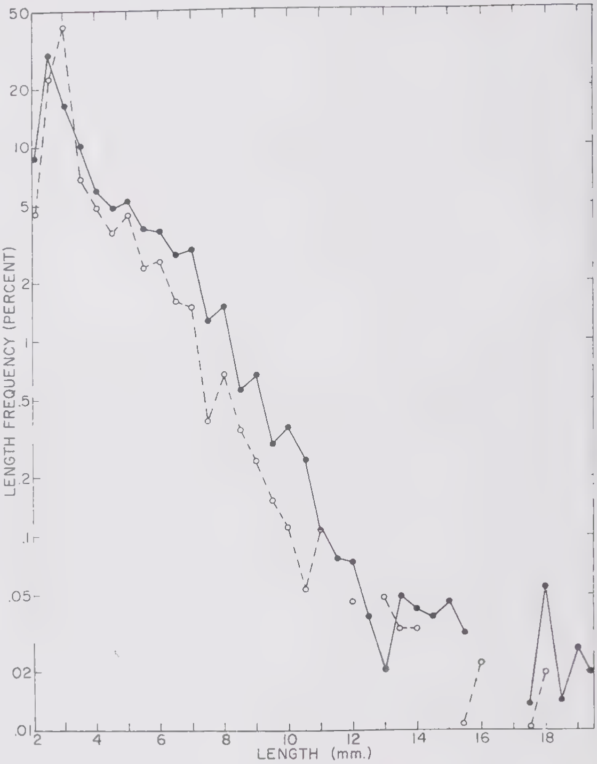

Figure 170. Catch curve of Pacific hake catches, 1966. Solid line indicates night catches. Dashed line indicates day catches.

JACK MACKEREL

The day and night catch curves of jack mackerel larvae captured during 1966 are shown in Figure 171. The modal size occurs at 3 mm in both curves. The two curves are nearly identical until catches become insignificant at 8·5 mm. There is a tendency for the night to day catch ratio to decrease at the larger sizes. Estimates of the parameters of equation (2) are given in Table 95. The model explains about 98% of the variance. Although the estimated value of C is significant ($P = 0{\cdot}05$), it is negative and low. It may be prudent to agree with the conclusion of Farris (1961) that there is not a significant relationship between the day to night ratio of jack mackerel larvae catches and size. If C is not included in the equation, the estimate of A remains the same and the estimate of B changes slightly to 1·12. In either case the catch rate during the day of jack mackerel larvae decreases about 67%

Table 94. Estimates of parameters of equation (2)

Species	Years	A	B	C	S_0	R
Pacific hake	1966	0·50	0·48	0·21	3·00	0·96
Jack mackerel....	1966	1·13	1·18	–0·11	3·00	0·99
Pacific sardine ...	1951	0·68	0·15	0·24	4·75	0·97
„ „ ...	1952	0·53	0·21	0·24	4·75	0·92
„ „ ...	1953	0·41	0·15	0·23	4·75	0·86
„ „ ...	1954	0·47	0·19	0·24	4·75	0·94
„ „ ...	1955	0·46	0·26	0·12	4·75	0·95
„ „ ...	1956	0·48	0·15	0·17	4·75	0·86
„ „ ...	1957	1·07	0·23	0·28	4·75	0·92
„ „ ...	1958	0·94	0·33	0·17	4·75	0·94
„ „ ...	1959	0·41	0·23	0·21	4·75	0·88
„ „ ...	1960	0·63	0·21	0·41	4·75	0·95
„ „ ...	1951–60	0·52	0·22	0·20	4·75	0·96
North. anchovy ..	1951	1·03	0·46	0·00	6·75	0·99
„ „ ..	1952	1·19	0·43	0·19	6·75	0·99
„ „ ..	1953	1·27	0·41	0·16	6·75	0·97
„ „ ..	1954	1·12	0·40	0·17	6·75	1·00
„ „ ..	1955	1·32	0·42	0·13	6·75	0·99
„ „ ..	1956	1·42	0·37	0·26	6·75	0·98
„ „ ..	1957	1·23	0·41	0·08	6·75	0·98
„ „ ..	1958	1·20	0·41	0·17	6·75	1·00
„ „ ..	1959	1·12	0·32	0·22	6·75	0·99
„ „ ..	1960	1·13	0·39	0·26	6·75	1·00
„ „ ..	1951–60	1·28	0·42	0·16	6·75	1·00
Northern anchovy (separated by subpopulations)						
northern	1951–60	1·22	0·38	0·14	6·75	1·00
southern	1951–60	1·43	0·46	0·23	6·75	0·99

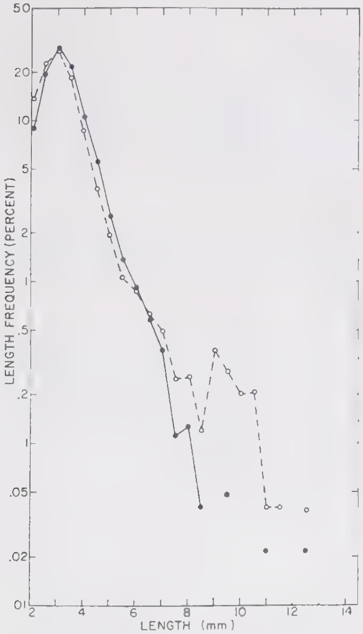

Figure 171. Catch curve of jack mackerel larvae, 1966. Solid line indicates night catches. Dashed line indicates day catches.

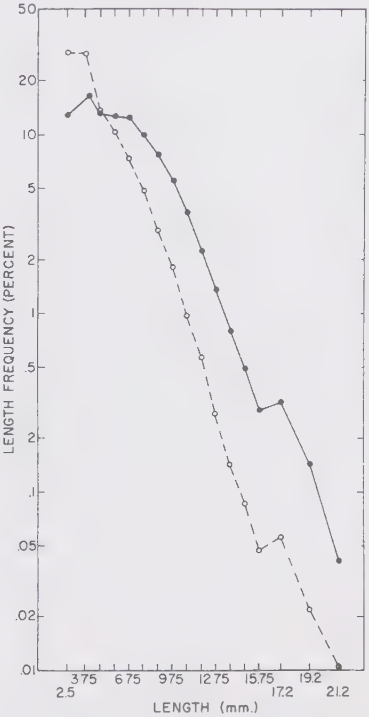

Figure 172. Catch curve of Pacific sardine larvae 1951–60. Solid line indicates night catches. Dashed line indicates day catches.

per mm of growth. Ahlstrom (pers. comm.) has estimates of catch by size of jack mackerel larvae from 1952, 1953, and 1954. Differences in effort by month and area were adjusted. These data indicate that B should be about 0·85. In this case the catch rate decline is about 57% per mm of growth.

PACIFIC SARDINE

For Pacific sardine larvae collected during 1951–1960 (Fig. 172), modal size is at 3 mm for day catches and 4·75 mm for night catches. The size increment is increased at 17·25 mm because of a scarcity of larvae beyond this size. There is a slight increase in catch rate at 17·25 mm over the preceding size because of the change in increment. This artefact could be partially corrected by dividing the catch rate of larvae greater than 15·75 mm by two. However, the average size of larvae captured in the intervals of concern is not evident *a priori* because of the exponential decline in catch rate. Thus, Pacific sardine larvae, and northern anchovy larvae, larger than 15·75 mm are not included in the analysis. There is a tendency for the slopes to be greater between 4·75 mm and 6·75 mm than between 6·75 mm and 15·75 mm. This tendency

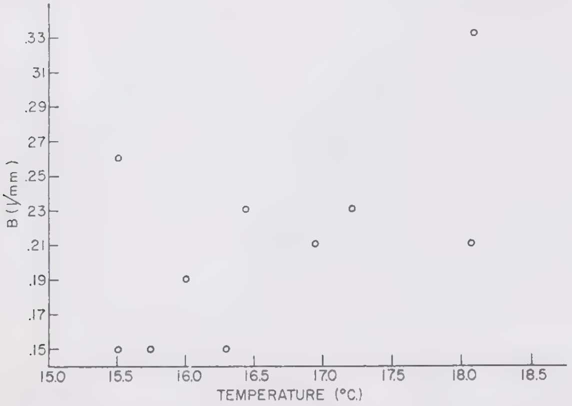

Figure 173. Estimates of *B* for Pacific sardine and average temperature at 10 m.

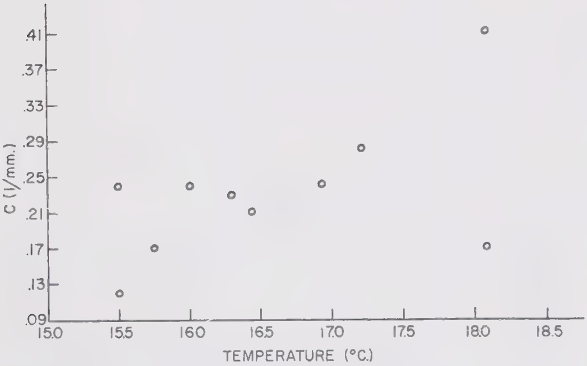

Figure 174. Estimates of *C* for Pacific sardine and average temperature at 10 m.

appears in most of the years that were examined. However, for the sake of simplicity the slopes are assumed to be constant between 4·75 mm and 15·75 mm. The concavity between 4·75 mm and 15·75 mm of the day curve (Fig. 172) did not appear in a consistent fashion during the years studied and is assumed to be unimportant.

Estimates of the parameters of equation (2) are given in Table 94 for each year and for all of the years combined. The estimate of *B*, for all years combined, is 0·22 and the range 0·15–0·33. This indicates that the catch rate of Pacific sardine at night declines about 20% per mm of growth. The model explains about 92% of the variance of the combined data.

It is plausible that *B* and *C* are related to temperature for several reasons including temperature-specific growth and predation rates. Average temperatures at 10 m were calculated for each year by weighting observed temperatures by catches of larvae. Temperatures at 10 m depth are used because data of Ahlstrom (1959) indicate that this is the average depth of Pacific sardine larvae. The temperatures are shown in Table 95.

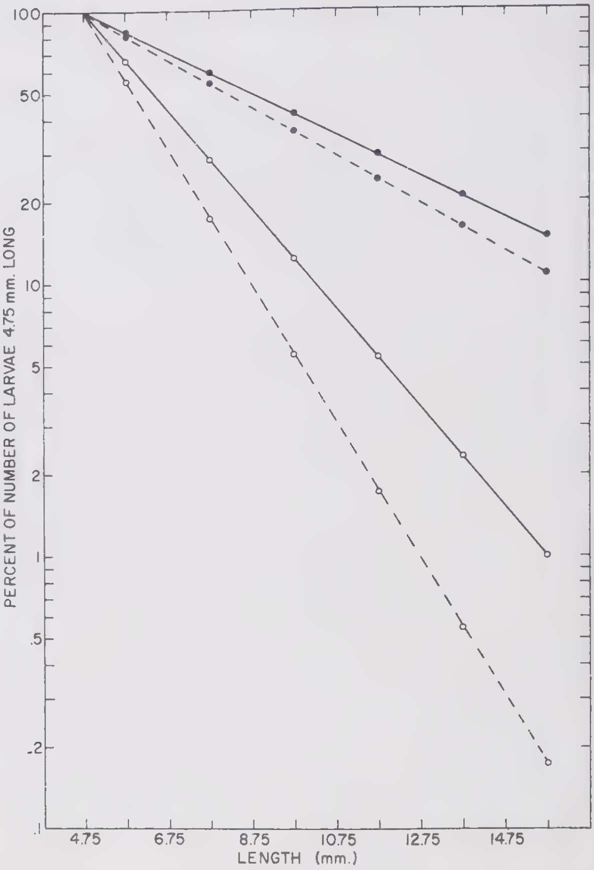

Figure 175. Percentage of number of Pacific sardine larvae 4·75 mm long captured at indicated size as predicted by equation (4) at temperatures of 15·5°C (solid line) and 18°C (dashed line). Open circles indicate day catches. Closed circles indicate night catches.

Plots (Fig. 173, 174) of *B* and *C* against temperature indicate a linear relationship. Thus, equation (2) was modified by replacing the parameters *B* and *C* with linear relations reflecting their dependence on temperature. The parameters of the modified equation were then estimated by multiple linear regression. The results are significantly better ($P = 0{\cdot}01$) than the results from using equation (2). About 80% of the variance in the dependent variable is explained by the model. Figure 175 illustrates catches of Pacific sardine larvae predicted by the model at temperatures of 15·5°C and 18·0°C, the extremes encountered in the study. Temperature appears to have less effect on catch rate than light.

Table 95. Average temperatures at 10 m weighted by number of Pacific sardine larvae captured

Year	Average temperature (°C)
1951........	15·48
1952........	16·93
1953........	16·30
1954........	16·00
1955........	15·50
1956........	15·74
1957........	17·21
1958........	18·09
1959........	16·43
1960........	18·09

NORTHERN ANCHOVY

Catch curves of northern anchovy larvae captured during 1951–1960 (Fig. 176) show a modal size of 2·5 mm for day catches and 3·75 mm for those at night. Catches at night remain fairly constant until the size of 6·75 mm. Thus anchovy larvae less than 6·75 mm are not included in the analysis. Both curves decline in a nearly exponential fashion between 6·75 mm and 15·75 mm. However, there is a slight tendency for the rate of decline to increase with size.

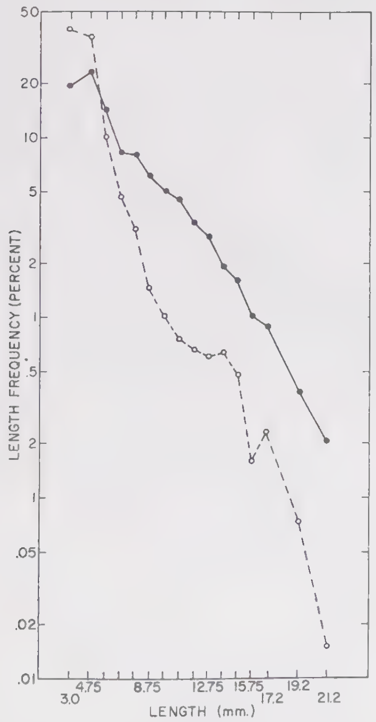

Figure 176. Catch curve of ~~northern~~ anchovy larvae, 1951–60. Solid line indicates night catches. Dashed line indicates day catches.

The estimate of B for all years combined is 0·39. This means that the catch rate during the day declined about 32% per mm of growth. About 99% of the variance is explained by the model. As in the case of the sardine larvae there are considerable differences among the estimates of B (0·32–0·46) and C (0·0–0·26) during the years studied. The parameters of the modified version of equation (2) were estimated using average temperatures at 10 m. The results were not significant. The work of Ahlstrom (1959) indicated that the average depth of northern anchovy larvae is about 20 m. Unfortunately, temperatures at this depth are not available at the present.

There is strong evidence for the existence of at least two sub-populations of northern anchovies (A. M. Vrooman, pers. comm.). The sub-populations are separated in the area of Cape Colnet, Baja California. It seemed possible that the sub-populations contributed to the variability in B and C. Therefore, I separated the catches of anchovy larvae into northern and southern sub-populations at obvious discontinuities in the distributions of the catches. These discontinuities occurred between the U.S.-Mexican border and Punta Eugenia, Baja California. Estimates of the parameters of equation (2) for the two sub-populations are shown in Table 94. The estimates of both B and C are higher for the southern than for the northern sub-population. About 99% of the variability is explained by the model in both cases.

DISCUSSION

There are considerable differences among the estimates of B (rate of decline) for the four species. Jack mackerel have the highest estimate, 1·18, while the Pacific sardine have the lowest, 0·22. It is interesting to note that recent work by K. Lillelund (pers. comm.) showed that predation on newly hatched sardine larvae by *Labidocera* is less than that on newly hatched anchovy larvae. With the exception of jack mackerel, the estimates of C (rate of increase of night to day catch ratio) are quite similar, at about 0·2. Farris (1961) attributed the lack of a relationship between size and the night to day ratio of catches of jack mackerel to a lack of avoidance by jack mackerel to capture. It seems unlikely that jack mackerel larvae do not avoid capture, since they are more developed structurally at small sizes than the other species studied. Also, the estimate of B is highest for jack mackerel. It is more likely that mackerel larvae are able to avoid capture equally well by day and night. With this in mind it does not seem prudent to interpret the rate of decline of night catches, as a mortality rate. Ahlstrom (pers. comm.) has examined the night to day ratios of catch rates of larvae of numerous species of fish and observed that the night to day ratio of jack mackerel appears to be unique for fish that inhabit the euphotic zone.

The growth rate may also contribute to *B*. The time spent in a size interval is dependent on growth rate. Since this rate has been shown to be related to temperature, the relation between estimates of *B* and temperature may be partially caused by different growth rates. Unfortunately, we do not have sufficient data on growth and temperature to come to any conclusions regarding the contribution of growth to *B*. Some work has been done on Pacific sardine growth at small sizes (<7 mm) at temperatures encountered in the present study. We also have some data on Pacific sardines at larger sizes at higher temperatures than encountered in the study. J. Zweifel (pers. comm.) has extrapolated these data to the temperatures encountered in the study. The dependence of *B* on temperature is shown to some extent by using these data for larvae between 5 and 11 mm.

The demonstrated differences among the catch curves can have significant effects on the catches of fish larvae, summed over size. For example, given equal numbers of newly hatched larvae, one would expect to catch fewer jack mackerel larvae than sardine larvae because of the difference in their rates of decline. Also, northern anchovy larvae appear to be fully retained at considerably larger sizes than the other species. The flat area of the catch curve of anchovy between 4·75 mm and 6·57 mm (Fig. 176) may be explained if the rate of decline cancels out the increased retention by the net. To study the effect on total catch, I set the number of larvae captured at the smallest size to one for Pacific sardine, jack mackerel, and Pacific hake, then corrected for changes in size increment of the smallest size, and used equation (2) to estimate the catches summed over size up to 15·75 mm. I also corrected for the apparently low retention rate in the case of anchovy larvae. Assuming that the ratio of night to day hauls is one, the total catches would be

Pacific sardine	3·4
Pacific hake	2·3
jack mackerel	1·5
northern anchovy	1·0

The implications of these figures on estimates of spawning stock size made from total number of larvae are obvious. The problem is not as serious when relative strengths of year classes of the same species are estimated.

The results of this study suggest that there are serious sources of error in the use of total numbers of larvae for the estimate of spawning stocks. Attempts to correct for these sources of error can be made in the fashion described in the preceding paragraph. It would be preferable to determine experimentally rates of growth, retention, and avoidance. It should be possible to determine size-specific rates of retention and avoidance with the use of plankton nets of different mesh and mouth sizes.

ACKNOWLEDGEMENTS

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7322

ESTIMATION OF RATES OF TAG SHEDDING BY NORTHWEST ATLANTIC BLUEFIN TUNA[1]

A joint experiment was initiated by the Fisheries Research Board of Canada (FRBC), the National Marine Fisheries Service, and the Woods Hole Oceanographic Institution (WHOI) in 1971 under the leadership of F. Mather to estimate the rates of tag shedding by bluefin tuna. Five hundred and eighty bluefin tuna were double tagged with one of four types of dart tags off the east coast of the U.S. during the 1971 fishing season. Two types of darts, metal and plastic, were used and tags supplied by FRBC were slightly different from tags supplied by WHOI. Tags and tagging procedures

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TABLE 1.—Tag releases and returns from east coast of U.S. bluefin tuna double tag study.

Agency and tag type	1971 Double tag releases	1971 First year returns n_{dd1}	n_{ds1}	t_1 (days)	1972 Second year returns n_{dd2}	n_{ds2}	t_2 (days)
FRBC							
Plastic dart	140	16	1	24.4	7	8	369.8
Metal dart	128	9	1	19.4	9	11	376.0
WHOI							
Plastic dart	150	4	0	7.2	20	9	349.9
Metal dart	162	4	1	18.6	10	9	371.1
Total							
Plastic dart	290	20	1	19.8	27	17	357.3
Metal dart	290	13	2	19.1	19	20	373.7
Total	580	33	3	19.5	46	37	364.7

were those described by the Food and Agriculture Organization (1972). The 1971 releases and returns in 1971 and 1972 are shown in Table 1 by tagging agency and dart type.

The notation and methodology in this study follows Bayliff and Mobrand (1972):

$$n_{ddk} = F\tau N_D \pi \rho^2 e^{-(F + X + 2L)t_k}$$

$$n_{dsk} = F\tau N_D \pi \rho (1 - \rho e^{-L t_k}) e^{-(F + X + L)t_k}$$

where:

t_k = time at the middle of the kth period of length τ ($k = 1, 2$),

n_{ddk} = number of returns of double-tagged fish retaining both tags during the period centered at t_k,

n_{dsk} = number of returns of double-tagged fish retaining only one tag during the period entered at t_k,

N_D = number of fish released with double tags,

π = portion of tagged fish which remain alive after the Type-I (immediate) mortality has taken place,

ρ = portion of the tags which are retained after Type-I (immediate) shedding has taken place,

F = instantaneous rate of fishing mortality,

X = instantaneous rate of other mortality (other includes natural mortality, Type-II (long-term) tagging mortality and apparent mortality caused by migration from the fishery), and

L = instantaneous rate of shedding of tags.

Bayliff and Mobrand showed that

$$\ln \frac{2n_{ddk}}{n_{dsk} + 2n_{ddk}} = -Lt_k + \ln\rho = Y_k$$

where Y_k is an estimate of the log of the proportion of tags retained up to time t_k.

Estimates of Y_k are shown in Table 2. Estimates of L and ρ are shown in Table 3. Although some differences among categories are indicated, a chi square test for differences in returns among categories was not significant at the 90% level of confidence. Thus the differences do not appear to be large enough to rule out the use of

TABLE 2.—Intermediate results in estimates of shedding rates from 1971 U.S. east coast bluefin double tag study.

Agency and tag type	Y_1	Y_2
FRBC		
Plastic dart	-0.03077	-0.45199
Metal dart	-0.05407	-0.47692
WHOI		
Plastic dart	0	-0.20294
Metal dart	-0.11778	-0.37156
Total		
Plastic dart	-0.02469	-0.27370
Metal dart	-0.07411	-0.42286
Total	-0.04445	-0.33802

TABLE 3.—Estimates of ρ and L from 1971 U.S. east coast bluefin double tagging study.

Agency and tag type	$\ln\rho$	L on daily basis	ρ	L (on annual basis)
FRBC				
Plastic dart	-0.00102	0.0012195	0.999	0.44512
Metal dart	-0.03106	0.0011858	0.969	0.43282
WHOI				
Plastic dart	0.00426	0.0005922	1.004	0.21615
Metal dart	-0.10439	0.0007199	0.901	0.26278
Total				
Plastic dart	-0.01008	0.0007378	0.990	0.26929
Metal dart	-0.05532	0.0009835	0.946	0.35898
Total	-0.02787	0.0008504	0.973	0.31041

the estimates obtained from the combined data. These estimates of $\rho = 0.973$ and $L = 0.31041$ are close to the estimates of Bayliff and Mobrand (1972) of $\rho = 0.913$ and $L = 0.278$ for yellowfin tuna in the eastern Pacific.

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7323

COMPARATIVE STUDY OF ADAPTATIONS FOR CONTINUOUS SWIMMING AND HYDROSTATIC EQUILIBRIUM OF SCOMBROID AND XIPHOID FISHES

JOHN J. MAGNUSON[1, 2]

ABSTRACT

Scombroid fishes swim continuously with pectoral fins extended as lifting hydrofoils to counter their weight in water. Their gas bladder is often reduced or absent. Typical speeds were observed from seven species and compared with the speeds expected from them to maintain hydrostatic equilibrium. The expected speeds were computed from a model I developed using data on the lifting area of extended pectoral fins and the weight of the fish in water.

Lifting areas of the pectoral fins were determined from photographs of dead fishes. Mass-length relations were determined and converted to weight in water from data on water density and fish density.

Typical observed speeds varied among species from 0.33 to 2.19 lengths/sec. Scombroids of the same fork length differed greatly in mass, density, and pectoral fin areas. Swimming speed required for maintaining hydrostatic equilibrium should be greater for fishes with greater mass, higher density, and smaller pectorals. Expected speeds were computed. They were highly correlated with observed speeds, $r = +0.89$. Thus, the model accurately predicted typical swimming speeds of scombroids, which suggests that variations in mass, density, and the lifting area of the pectoral fins, through the mechanism of maintaining hydrostatic equilibrium, can account for about 80% of the variation in typical swimming speeds. Expected speeds (centimeters per second) generated from the model either increased with fork length or reached a maximum and declined for larger fish. The latter pattern occurred if gas bladders were relatively larger in older fish or even absent in younger fish.

Scombroids with faster typical speeds have larger dark muscles and higher concentrations of blood hemoglobin than those with slower speeds. Differences in body shape were not closely related to differences in typical speeds.

Larger fishes should have more difficulty maintaining a speed which is sufficient for hydrostatic equilibrium without a gas bladder or large pectoral fins. The occurrence of gas bladders and long pectoral fins were compared for small, medium, and large scombroid and xiphoid fishes. Both were more common among larger species. Each species with a maximum mass $\geqslant 70$ kg had a gas bladder while only 26% of those species $\leqslant 6$ kg had a gas bladder. Further analyses suggested that a gas bladder and large pectorals may be increasingly more important for large species if they are to swim at energetically prudent speeds.

Scombroid fishes are negatively buoyant, pelagic, oceanic fishes. The scombroids include the mackerels, tunas, and bonitos. They swim continuously with pectoral fins extended. This behavior produces lift that balances their weight in water. Some attain large size. Xiphoids are the largest teleosts and powerful swimmers that share the pelagic environment with the scombroids.

General considerations of buoyancy mechanisms of negatively buoyant fishes are discussed by Aleev (1963) and Alexander (1967, 1968).

In regard to scombroids, Magnuson and Prescott (1966) observed that continuous swimming was apparently not entirely determined by a need for gill ventilation, as Pacific bonito,

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Sarda chiliensis, swam with their mouth closed as much as 40% of the time. Presumably the fish could have conserved energy by swimming more slowly with the mouth open more often. Minimum speed was also not regulated for food search (Magnuson, 1969); kawakawa, *Euthynnus affinis*, swam at the same speed day and night even though they were exclusively diurnal feeders. When deprived of food for several days, they swam slower and slower in absence of food stimuli. If typical speed had been regulated by feeding motivation, the fish would have been expected to swim faster—become more active—as motivation to feed increased.

Typical swimming speeds of *E. affinis* were well explained by the minimum speed required to produce sufficient lift on the pectoral fins to keep from sinking. Magnuson (1970) presented a model to predict minimum speed required of *E. affinis* to maintain hydrostatic equilibrium. Minimum speeds were estimated from the animal's weight in water and the lifting area, primarily of the pectoral fins.

Differences between the morphology and typical speeds of yellowfin tuna, *Thunnus albacares*, and *E. affinis* (Magnuson, 1966a) suggested that the variations in area of pectoral fins and volume of gas bladder might also be explained as various solutions for countering negative buoyancy. Many other specializations of scombroids related to swimming speed and activity may be adaptations to the speeds required for hydrostatic equilibrium rather than maximum, burst speeds (Magnuson, 1970).

In regard to xiphoids, a recent review on their functional morphology by Ovchinnikov (1970) did not consider the gas bladder or buoyancy mechanisms in discussions on the function of pectoral fins.

Purposes of the present paper are to (1) test whether the model mentioned above generally predicts typical swimming speeds of scombroid fishes, (2) consider the adaptive radiation in the morphology especially of the gas bladder and pectoral fins which together with swimming speed contribute to the mechanism by which scombroids maintain hydrostatic equilibrium, and (3) consider problems associated with large body size and maintenance of hydrostatic equilibrium among scombroid and xiphoid fishes.

SWIMMING SPEEDS

Typical swimming speeds were observed for five scombroid fishes in 7.2-m diameter swimming pools at Kewalo Basin, Honolulu, Hawaii, from underwater photographs of wahoo, *Acanthocybium solandri*, swimming at sea, and from previously published records on *Sa. chiliensis* (Magnuson and Prescott, 1966). Observed swimming speeds were determined or available for seven species of six different genera.

Methods for obtaining swimming speeds were described by Magnuson (1969). Fishes were observed for short periods at 1- to 4-hr intervals (0000-2400) during their first month in captivity. Observations were made for two consecutive 24-hr periods during which the fish were fed and not fed (Figure 1). On fed days they were fed to satiation with thawed smelt or shrimp once or twice usually at 0900 and 1600 hr. Data collected during the "day not fed" and the "night after not fed" were used for the estimates of the minimum typical swimming speed to compare with body morphology. These estimates were based on 19-212 min (median 68 min) of recorded speeds for each species. With the exception of 36-cm long bigeye tuna, *Thunnus obesus*, where only 1 fish was observed, measurements from 6 to 40 fish (median 12 fish) made up each estimate. Water temperatures were 23°-26°C and salinity $33\,^{0}/_{00}$.

Typical speeds of *Ac. solandri* were from 17 cinema sequences averaging 2.59 sec each. The films were taken from underwater viewing ports in the RV *Charles H. Gilbert* and an observation raft described in Nakamura (1972).

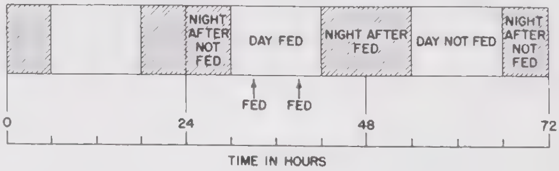

FIGURE 1.—Observation schedule for measurements of typical swimming speeds presented in Figure 2.

The observations that scombroid fishes swim continuously (Figure 2) would appear to be generalizable but the speeds, expressed either as body lengths per second (*l*/sec) or centimeters per second (cm/sec), differ considerably from one species to another or within species depending upon the size. Typical speeds ranged from 0.33 *l*/sec for *Ac. solandri* to 2.19 *l*/sec for the bullet mackerel, *Auxis rochei*. All species other than *Ac. solandri*, namely the skipjack tuna, *Katsuwonus pelamis*, *Sa. chiliensis*, *E. affinis*, *T. obesus*, *T. albacares*, and *Au. rochei*, had typical speeds greater than 1 *l*/sec. None of the species ever stopped swimming. The slowest speeds observed ranged from 0.12 *l*/sec for *Ac. solandri* to 1.97 *l*/sec for *E. affinis*. The typical speed of *T. obesus*, 36 cm FL (fork length), was 1.31 *l*/sec but the larger 55-cm *T. obesus* swam only 1.08 *l*/sec. Three length groups of the *K. pelamis* were also observed and their speeds differed among sizes.

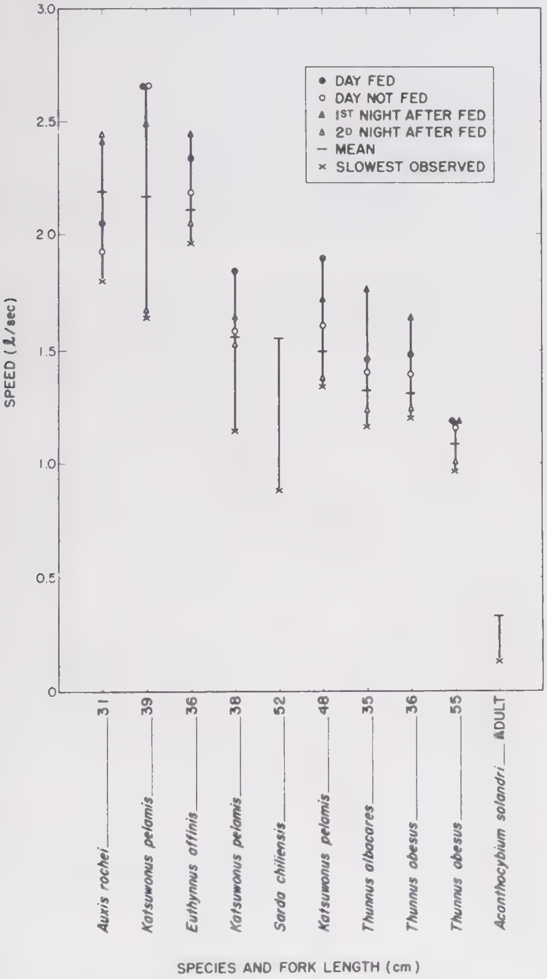

FIGURE 2.—Typical swimming speeds of seven scombroids.

SPEEDS REQUIRED FOR HYDROSTATIC EQUILIBRIUM

Variations in the typical swimming speeds among scombroids would result from differences in both the weight of the fish in water and the lifting area of the pectoral fins. Weight in water depends on mass and density of the fish. All specimens of chub mackerel, *Scomber japonicus*, and *Sarda chiliensis* used for morphometric and mass measurements were collected near Los Angeles, Calif. Specimens of all other species were collected in the central Pacific almost always near the Hawaiian Islands.

Variations in Weight

Not all scombroids have the same mass-length relationship (Figure 3). *K. pelamis* was heaviest and *Ac. solandri* lightest at a given length. For example, at a length of 75 cm, *Ac. solandri* has a mass less than 2 kg and *K. pelamis* greater than 9 kg. Other species were intermediate.

When submerged in water the fish displaces water which also has mass. If the gas bladder is large enough, the volume of water that a fish displaces may have the same mass as the fish. The weight of the fish in water, or conversely the lift required to keep the fish from sinking, is equal to the excess mass of the fish times the acceleration of gravity (Alexander, 1967; Magnuson, 1970). The excess mass of the fish is the difference between the mass of the fish and the mass of the water it displaces. It can be computed by multiplying the mass of the fish by $(1 - \frac{D_e}{D_f})$ where D_e is the density of the environment or seawater and D_f is the density of the fish. The

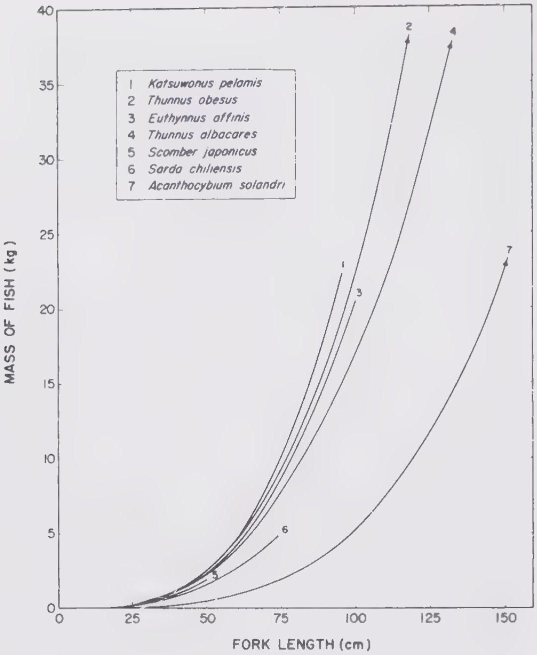

FIGURE 3.—Comparison of mass against length relationships among seven scombroid species. Information on regression equations in Table 4.

acceleration of gravity, g, is equal to approximately 980 cm/sec^2.

The influence of a gas bladder can be clearly seen by contrasting data for *K. pelamis* with *T. albacares*. Gas bladder volumes were determined with an x-ray method of Chang and Magnuson (1968) on fish immediately after they were killed. *K. pelamis* has no gas bladder but *T. albacares* has a gas bladder which grows allometrically, becoming progressively larger as the fish increases in mass (Figure 4a). *T. albacares*, 2 kg or less, has no gas in the bladder, but the gas bladder then grows rapidly until the fish is at least 8 kg. These differences in gas bladders of *K. pelamis* and *T. albacares* influence the density of the two species (Figure 4b). The density of *K. pelamis* remains approximately the same over the entire size range. However, once the gas bladder begins to grow in *T. albacares* the density of the fish becomes less, decreasing from approximately 1.09 g/ml for 2-kg fish to 1.05 g/ml for 10-kg fish. These differences in density have a corresponding influence on the lift required to keep the fish from sinking (Figure 4c). The lift required for *K. pelamis* increases in almost direct proportion to the increase of mass. But the lift required to keep *T. albacares* from sinking increases more slowly as the density of the fish becomes less. In fact, the lift required to keep *T. albacares* from sinking appears to approach asymptotically a maximum near 200 × 10^3 dynes.

Variations in the densities of various species and sizes can be examined in Table 1, where the mean densities of various species are given and the multipliers are computed to convert the mass of the fish to the lift required to keep them from sinking. All species with markedly lower densities, such as *Sc. japonicus*, *T. albacares*, *T. obesus*, and *Ac. solandri*, have gas bladders at some point in their life history. The more dense species, *Sa. chiliensis*, *Au. rochei*, *E. affinis*, and *K. pelamis*, have no gas bladder.

Lift to prevent the fish from sinking is 10 to 20 times greater for larger *K. pelamis*

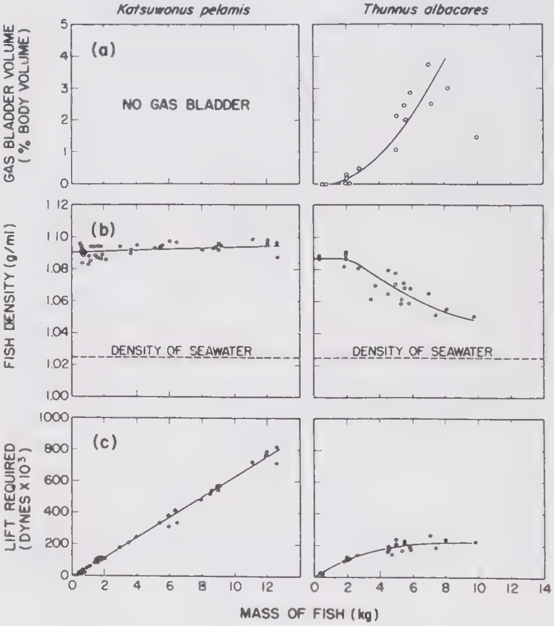

FIGURE 4.—Comparisons between *Katsuwonus pelamis* and *Thunnus albacares* of the relations between fish mass and (a) gas bladder volume, (b) fish density, and (c) lift required for hydrostatic equilibrium.

TABLE 1.—Densities (D_f) of eight scombroid species by size group and the multipliers to convert mass of fish (M_f in grams) to the lift (L in dynes) required for hydrostatic equilibrium. Multipliers[1] computed for seawater with densities of 1) 1.022 g/ml and 2) 1.025 g/ml. Measurements by methods described by Magnuson (1970).

Mass	*Scomber japonicus*	*Acanthocybium solandri*	*Sarda chiliensis*	*Auxis rochei*	*Euthynnus affinis*	*Katsuwonus pelamis*	*Thunnus albacares*	*Thunnus obesus*
0.00-1.99 kg:								
Number of fish	18		3	12	36	47	3	1
D_f (g/ml):								
Mean	1.054		1.075	1.086	1.087	1.090	1.086	1.066
SD	0.011		0.004	0.002	0.004	0.003	0.003	
Range	1.024		1.069	1.082	1.074	1.083	1.082	
	1.069		1.080	1.089	1.093	1.096	1.088	
Multiplier (1)	28.0		48.4	57.8	58.6	61.2	57.8	40.5
(2)	28.0		45.7	55.1	56.0	58.5	55.1	37.7
2.00-3.99 kg:								
Number of fish			10		23	4	4	17
D_f (g/ml):								
Mean			1.080		1.088	1.090	1.087	1.047
SD			0.006		0.009	0.003	0.004	0.010
Range			1.067		1.082	1.086	1.081	1.026
			1.086		1.094	1.094	1.090	1.064
Multiplier (1)			52.7		59.5	61.2	58.6	23.4
(2)			50.0		56.8	58.5	56.0	20.7
4.00-5.99 kg:								
Number of fish					3	4	12	
D_f (g/ml):								
Mean					1.091	1.094	1.068	
SD					0.004	0.001	0.007	
Range					1.086	1.093	1.059	
					1.095	1.095	1.080	
Multiplier (1)					62.3	64.6	42.2	
(2)					59.3	61.8	40.0	
6.00-7.99 kg:								
Number of fish						2	2	
D_f (g/ml):								
Mean						1.097	1.058	
SD						0.000	0.006	
Range						1.097	1.052	
						1.097	1.065	
Multiplier (1)						67.0	33.4	
(2)						64.4	30.6	
8.00-9.99 kg:								
Number of fish						6	2	
D_f (g/ml):								
Mean						1.094	1.054	
SD						0.001	0.002	
Range						1.093	1.051	
						1.096	1.056	
Multiplier (1)						64.6	29.8	
(2)						61.8	27.1	
≥10.00 kg:								
Number of fish		7				5		
D_f (g/ml):								
Mean		1.028				1.096		
SD		0.007				0.004		
Range		<1.022				1.088		
		1.042				1.099		
Multiplier (1)		5.78				66.3		
(2)		2.94				63.5		
All sizes (without gas bladders only):								
Number of fish			13	12	62	68		
D_f (g/ml):								
Mean			1.078	1.086	1.087	1.091		
SD			0.006	0.002	0.004	0.004		
Range			1.067	1.082	1.074	1.083		
			1.086	1.089	1.095	1.099		
Multiplier (1)			51.0	57.8	58.6	62.0		
(2)			48.2	55.1	56.0	59.3		

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[1] $[(1 - \frac{D_e}{D_f})980]$ where D_e is the density of environment.

(no gas bladder) than for *Ac. solandri*, which has a large gas bladder. These differences would also significantly influence the speed required to maintain hydrostatic equilibrium, and on this basis species without gas bladders are expected typically to swim faster than those with gas bladders.

Variations in the Lifting Area of Pectoral Fins

The lift produced by a hydrofoil is directly proportional to its lifting area, thus those species with a larger lifting surface should be capable of swimming at a slower speed, all other things being equal. The primary lifting surfaces of *E. affinis* are the pectoral fins (Magnuson, 1970), although other surfaces such as the caudal keel may counter some of the weight. The lifting area of the pectoral fins is the area of the extended pectoral fins as viewed from above plus the area of the body between the fins. It was determined for the various species from photographs of dead fish as described by Magnuson (1970).

Pectoral fins of scombroids are analogous to variable sweepback wings; they can be fully extended, swept back, or laid against the body (Magnuson, 1970). Species such as *E. affinis* and *K. pelamis* swam with the fins swept back about 40°, but the two species with the largest pectoral fins, *T. albacares* and *T. obesus*, swam with the fins swept back about 60° (Table 2). Sweepback angles measured from dead fish used for morphometric measurements were not as great as those from fish swimming in tanks. Measurements from dead fish were 7° and 14° for *E. affinis* and *K. pelamis* and 29° and 36° for *T. albacares* and *T. obesus*. Thus, some bias occurs in the estimation of the lifting area for swimming fish from the dead fish. This bias is probably slight because, although the actual area of the pectoral fin decreases rapidly as the fins are swept back, the total lifting area does not (Magnuson, 1970). Measurements of sweepback from other dead fishes used for morphometric measurements averaged 10° for *Sc. japonicus*, 24° for *Ac. solandri*, 16° for *Sa. chiliensis*, and 10° for *Au. rochei*.

Differences in pectoral fin lifting areas among scombroids are illustrated in diagrammatic dorsal views of seven species at the same length (Figure 5). Lifting areas differ markedly among species and among sizes for the same species (Figure 6). *T. obesus* has, among the species here, the largest lifting

TABLE 2.—Average sweepback of pectoral fins for swimming captive fishes. *n* equaled the number of fish. Λ was averaged for left and right fins.

Species	Day fed			Day not fed[1]			Fed and not fed combined		
	Λ (degrees)		*n*	Λ (degrees)		*n*	Λ (degrees)		*n*
	Mean	SD		Mean	SD		Mean	SD	
Euthynnus affinis	34	8.5	15	32	12	15	43	10	30
Katsuwonus pelamis	43	15	101	43	13	53	43	14	154
Thunnus albacares	61	3.1	11	55	3.7	3	60	4.0	14
Thunnus obesus	61	5.0	64	56	7.5	45	59	6.7	109

[1] Two days after fed for *E. affinis* and *T. albacares*; 1 day after fed for *K. pelamis* and *T. obesus*.

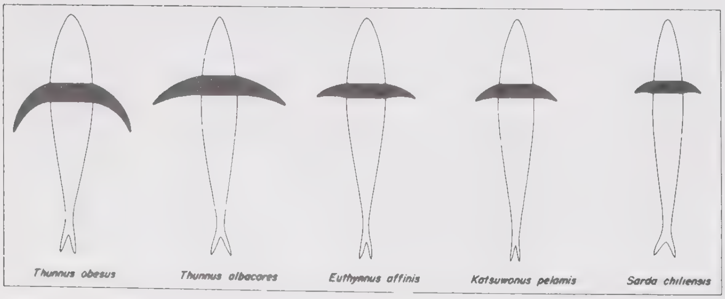

FIGURE 5.—Diagrammatic dorsal views of five scombroid species to dramatize the variation in the lifting areas of the pectoral fins for various species. Drawn from photographs of dead fish ca. 50 cm in fork length.

area at a given length, and *Ac. solandri* has the smallest. For example, at a fork length of 125 cm, *T. obesus* has a lifting area greater than 500 cm², whereas *Ac. solandri* has a lifting area near 150 cm² (Figure 6). These differences should have a marked effect on the minimum speed required to maintain hydrostatic equilibrium. Those with larger pectorals such as *T. albacares* and *T. obesus* should have a slower minimum speed than those with smaller pectorals.

Predicted Swimming Speed

The model used by Magnuson (1970) to predict the minimum speed required for hydrostatic equilibrium was

$$V_{100} = \left[\frac{L_t}{\rho/2\,(C_{L_f}A_{f_t} + C_{L_k}A_k)}\right]^{1/2}. \qquad (1)$$

All terms used here and elsewhere in this paper are listed below:

l = fork length (cm)
L_t = total weight of fish in water (dynes)
L_f = all lift produced by the total lifting area of the pectoral fins (dynes)
L_k = lift produced by keel (dynes)
A_{f_e} = area of pectoral fins
A_{f_t} = total lifting area of pectorals (cm²)
A_k = lifting area of keel (cm²)
C_{L_f} = coefficient of lift for the pectoral fins based on all lift produced by pectorals and on total lifting area of pectorals
C_{L_k} = coefficient of lift for the keel
V_{100} = speed of fish with pectorals continuously extended (cm/sec)
Λ = sweepback angle of pectoral fins (degrees)
D_e = ρ = density of water = 1.022 g/ml in Kewalo tanks, 1.025 g/ml at sea
D_f = density of fish (g/ml)
M_f = fish mass.

To test predictive value of this model for a number of species, computed speeds were compared with observed speeds. Typical swimming speeds were computed twice: first, assuming the keel provided significant lift, and second, assuming all the lift was provided by pectoral fins. Results from these computations and the data used to make them are presented in Table 3. Regressions in Table 4 were used to determine the mass of the fish and the area of the lifting surfaces for calculations of minimum hydrostatic speeds. The mass of the fish was converted to required lift by using the conversion factors from Table 1. Lift coefficients were from Table 7 of Magnuson (1970)—those determined for *E. affinis* on the basis of total lifting area of the pectorals.

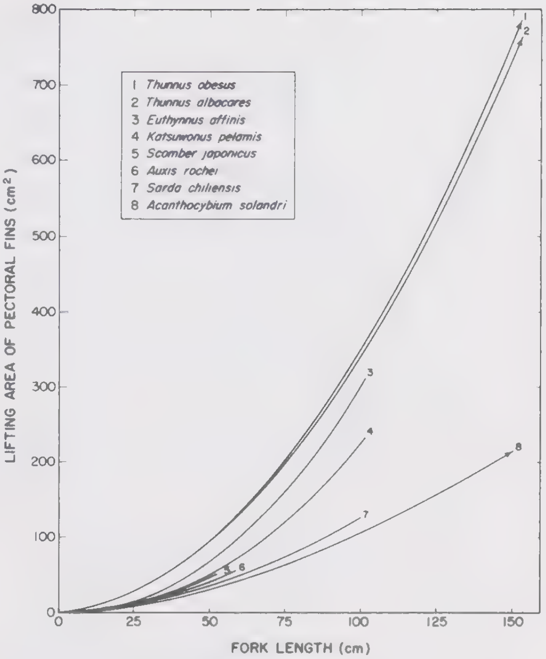

FIGURE 6.—Comparison of lifting area of pectoral fins against length relationships among eight scombroid species. Information on regression equation in Table 4.

Several comments should be made about the use of the lift coefficients from *E. affinis* for all species considered in the present text. The lift coefficient calculated on the basis of the total lifting area of pectorals represents lift on the pectorals, interference lift on the body owing to the pectorals, and the interference lift on the pectorals owing to the presence of the body. At best the coefficient is only a convenient but arbitrary standard frequently used in aerodynamic literature.

TABLE 3.—Computed speeds required for hydrostatic equilibrium and the morphometric data used to make the computations along with the typical swimming speeds observed for scombroids. Lift coefficients from Magnuson (1970). Masses, areas, and required lift from equations in Table 4 and fork length of captive fishes.

Species	l (cm)	(a) M_f (g)	(b) Multiplier to convert M_f to L_t	(a × b) L_t (dynes × 10³)	A_k (cm²)	(c) A_{f_t} (cm²)	Surface loading of pectorals ($L_t \div A_{f_t}$) (dynes/cm²)	Computed hydrostatic speeds (V_{100})[1] Without keel[2] (cm/sec)	(l/sec)	With keel[3] (cm/sec)	(l/sec)	Observed speed of fishes (cm/sec)	(l/sec)
Auxis rochei	31	498	57.8	28.8	[4]3.3	17.7	1,630	56	1.8	57	1.8	68	2.2
Katsuwonus pelamis	39	1,090	61.2	66.7	5.51	27.4	2,430	69	1.8	70	1.8	84	2.2
Euthynnus affinis	36	832	58.6	48.8	5.41	31.6	1,540	55	1.5	56	1.6	76	2.1
Katsuwonus pelamis	38	996	61.2	61.0	5.20	25.9	2,360	68	1.8	69	1.8	59	1.6
Sarda chiliensis	57	2,320	52.7	122.	11.8	45.9	2,660	72	1.3	71	1.2	88	1.5
Katsuwonus pelamis	48	2,180	61.2	133.	8.79	43.7	3,040	77	1.6	78	1.6	72	1.5
Thunnus albacares	35	858	57.8	49.6	6.11	47.0	1,060	45	1.3	47	1.4	46	1.3
Thunnus obesus	36	854	40.5	34.6	5.87	52.1	664	36	1.0	38	1.0	47	1.3
Thunnus obesus	55	3,290	23.4	77.0	15.8	116.	664	36	0.66	38	0.68	60	1.1
Acanthocybium solandri	125	[5]12,400	[6]5.78	71.7	51.6	163.	440	29	0.23	28	0.22	[7]41	0.33

[1] With equation 1. [2] $C_{L_k} = 0, C_{L_f} = 1.$ [3] $C_{L_k} = 0.9, C_{L_f} = 0.8.$

[4] Estimated by comparing data with *K. pelamis* and then taking from *K. pelamis* regression.

[5] Estimated from length-weight relation given by Iversen and Yoshida (1957).

[6] From Table 1, D_e = 1.022 g/ml.

[7] Speed (cm/sec) = speed (l/sec) × length (cm) = 0.33 × 125 = 41.

Lift coefficients vary with sweepback, angle of attack, aspect ratio, the ratio of fin span to body width, and taper ratio (Lawrence and Flax, 1954). The differences in these parameters among species or within species were not evaluated, but comparisons made below between observed and calculated speeds suggest that the assumption about a constant lift coefficient based on total lifting area was not too bad. The coefficients used here should be more accurate for scombroids with short pectorals because *E. affinis* has short pectorals. The span of the pectorals, tip to tip, for *E. affinis* is about 2.4 times the body width.

Correlation coefficients (Table 5) were computed to discover how closely the observed swimming speeds were associated with fork lengths of the fish, the mass of the fish, the required lift to keep the fish from sinking, the lifting area of pectoral fins, the surface loading of pectoral fins, and the predicted swimming speed. Relations between observed speed and fork length, mass of fish, required lift, and lifting area of the pectoral fins were all nonsignificant statistically. But when required lift and the lifting area were considered jointly as surface loading of the pectorals, the correlation was significant ($P <$ 0.005). Surface loading is the weight carried per unit area of lifting surface. Predicted speeds were also highly correlated with observed speeds (Table 5, Figure 7). The highest correlation, +0.89, between observed and predicted speeds in body lengths per second suggested that the hydrostatic equilibrium requirement of continuous swimming accounts for approximately 80% of the variation in observed swimming speeds. The model predicts typical swimming speeds of scombroids well and suggests that the variations in mass, density, and the lifting area of the pectoral fins can account for almost all variations in observed swimming speeds among scombroids.

Observed speeds averaged 9.8 cm/sec or 0.2 *l*/sec faster than computed speeds. The computation of V_{100} assumed that the pectorals were continuously extended but this was not always the case. Thus, the fact that observed speeds were greater than V_{100} is not surprising. *E. affinis*, for example, had the pec-

TABLE 4.—Regression equations ($\log y = \log a + b \log l$) with relevant data and 95% confidence intervals used to compute fish mass (M_f), area of pectoral fins (A_{fe}), lifting area of pectoral fins (A_{ft}), and keel area (A_k) for nine species of scombroid fishes. Measurements made by methods described in Magnuson (1970).

y	Species	n	Range in l (cm)	log l	log y	log a	a	b	S_b	SE est.	Confidence limit on b	Confid. limit on $\log y_{\overline{\log l}}$
M_f	*Sc. japonicus*	20	26.9- 41.4	1.5434	2.7630	−2.4353	0.00367	3.37	0.1458	0.0345	±0.31	±0.0725
	Ac. solandri	—	—	—	—	—	—	—	—	—	—	—
	Sa. chiliensis	13	45.3- 65.1	1.7524	3.3647	-1.4100	0.0389	2.72	0.1770	0.0284	±0.39	±0.0625
	Au. rochei	11	33.9- 40.4	1.5546	2.9038	-2.3143	0.00485	3.36	0.4557	0.0290		
	E. affinis	63	31.6- 67.8	1.6251	3.1383	-1.9666	0.0108	3.14	0.0388	0.0632	±0.08	±0.1265
	K. pelamis	68	24.1- 82.9	1.6395	3.1977	-2.3098	0.00490	3.36	0.0180	0.0212	±0.04	±0.0424
	T. albacares	52	28.4-106.9	1.7859	3.6236	-1.4828	0.0329	2.86	0.0420	0.0325	±0.08	±0.0653
	T. obesus	26	36.3-150.5	1.8421	3.8440	-2.0173	0.00961	3.18	0.0868	0.1606	±0.18	±0.3315
A_{fe}	*Sc. japonicus*	25	26.9- 40.1	1.5407	1.0005	-2.1543	0.00701	2.05	0.1864	0.0426	±0.39	±0.0881
	Ac. solandri	7	122.8-148.8	2.1112	1.9565	-2.1931	0.00641	1.97	0.7864	0.0551	±2.02	±0.1417
	Sa. chiliensis	13	45.3- 65.1	1.7524	1.3020	-2.2358	0.00581	2.02	0.4993	0.0800	±1.10	±0.1761
	Au. rochei	11	31.9- 40.4	1.5499	1.0380	-2.0348	0.00923	1.98	0.7455	0.0586	±1.69	±0.1326
	E. affinis	37	33.7- 64.3	1.6440	1.3759	-2.3010	0.00500	2.24	0.0940	0.0475	±0.19	±0.0964
	K. pelamis	33	24.3- 82.9	1.7271	1.3722	-2.3840	0.00413	2.17	0.0562	0.0477	±0.11	±0.0974
	T. albacares	32	28.4-148.8	1.7920	1.9453	-1.2351	0.0582	1.78	0.0631	0.0602	±0.13	±0.1229
	T. obesus	25	46.1-150.5	1.8496	2.0613	-1.0477	0.0896	1.68	0.0445	0.0828	±0.09	±0.1713
A_{ft}	*Sc. japonicus*	25	26.9- 40.1	1.5407	1.3394	-1.7012	0.0199	1.97	0.2520	0.0576	±0.65	±0.1481
	Ac. solandri	7	122.8-148.8	2.1112	2.2192	-1.5031	0.0314	1.76	0.5700	0.0399	±1.25	±0.0878
	Sa. chiliensis	13	45.3- 65.1	1.7524	1.6472	-1.4634	0.0344	1.78	0.3892	0.0613	±0.86	±0.1350
	Au. rochei	10	31.9- 40.4	1.5505	1.3546	-1.2418	0.0573	1.67	0.7115	0.0557	±1.64	±0.1284
	E. affinis	37	33.7- 64.3	1.6440	1.6920	-2.0182	0.00959	2.26	0.0855	0.0432	±0.17	±0.0877
	K. pelamis	33	24.3- 82.9	1.7271	1.7402	-2.1255	0.00749	2.24	0.0545	0.0462	±0.11	±0.0943
	T. albacares	32	28.4-136.0	1.7920	2.1402	-1.2154	0.0609	1.87	0.0478	0.0456	±0.10	±0.0931
	T. obesus	25	46.1-150.5	1.8496	2.2599	-1.2090	0.0618	1.88	0.0391	0.0366	±0.08	±0.0757
A_k	*Sc. japonicus*	—	—	—	—	—	—	—	—	—	—	—
	Ac. solandri	—	—	—	—	—	—	—	—	—	—	—
	Sa. chiliensis	13	45.3- 65.1	1.7524	1.0761	-1.2104	0.0616	1.30	0.4784	0.0766	±1.05	±0.1687
	Au. rochei	—	—	—	—	—	—	—	—	—	—	—
	E. affinis	41	33.7- 67.8	1.6479	0.9548	-3.0017	0.000996	2.40	0.1501	0.2477	±0.30	±0.5011
	K. pelamis	34	24.3- 82.9	1.7128	1.0154	-2.8386	0.00145	2.25	0.0761	0.1308	±0.16	±0.2667
	T. albacares	36	34.0-136.0	1.8005	1.3687	-2.7033	0.00198	2.26	0.0986	0.1786	±0.20	±0.3624
	T. obesus	25	46.1-150.5	1.8496	1.4489	-2.8729	0.00134	2.34	0.1284	0.2387	±0.27	±0.4940

TABLE 5.—Correlations between observed speeds of scombroids and the fork length, mass, required lift for hydrostatic equilibrium, surface loading, and computed speeds with and without the keel included in the calculation.

Correlates		r_{xy}	$P(n = 10)$
y	x		
V_{obs} (cm/sec)	Fork length (l) (cm)	-0.37	N.S.
V_{obs} (cm/sec)	Mass of fish (M_f) (g)	+0.44	N.S.
V_{obs} (cm/sec)	Required lift (L_t) (dynes)	+0.44	N.S.
V_{obs} (cm/sec)	Lifting area of pectorals (A_{f_t}) (cm^2)	-0.54	N.S.
V_{obs} (cm/sec)	Surface loading of pectorals (dynes/cm^2)	+0.77	<0.005
V_{obs} (cm/sec)	V_{100} without keel (cm/sec)	+0.79	<0.005
V_{obs} (cm/sec)	V_{100} with keel (cm/sec)	+0.78	<0.005
V_{obs} (l/sec)	V_{100} without keel (l/sec)	+0.89	<0.0005

torals extended only about 75% of the time at typical speeds. The percent of extension of the pectorals varied greatly from species to species. The species with the longest pectorals, *T. obesus* and *T. albacares*, almost never appressed their pectoral fins while swimming at typical speeds.

Typical speeds of each species over its length range (Figure 8) were computed from equation 1 using values for M_f, A_{f_t} from Table 4, and values of D_e from Table 1, ρ was set at 1.025 g/ml. Since the inclusion of lift from the keel had little effect on computed speeds (Table 3), the computations were made on the basis that all lift came from the pectorals.

The three species with the fastest predicted swimming speeds—*K. pelamis*, *Sa. chiliensis*, and *E. affinis*—have no gas bladder (Figure 8), while species with the lowest predicted speeds—*T. albacares*, *T. obesus*, *Sa. japonicus*, and *Ac. solandri*—have gas bladders. *Ac. solandri*, the species with the lowest predicted speed, has the largest gas bladder and the lowest density.

Among the three species without gas bladders, *K. pelamis* is the heaviest for its length and has the fastest minimum speed. The predicted speeds of *Sa. chiliensis* and *E. affinis* are quite similar, even though *E. affinis* is considerably heavier at a given length than *Sa. chiliensis* (Figure 3). This difference results from the difference in the lifting area of pectoral fins (Figure 6). *E. affinis* has lifting areas twice the size of *Sa. chiliensis* at a given length. Interestingly, the minimum speeds predicted for *K. pelamis* were almost identical to the speeds predicted by Shuleikin

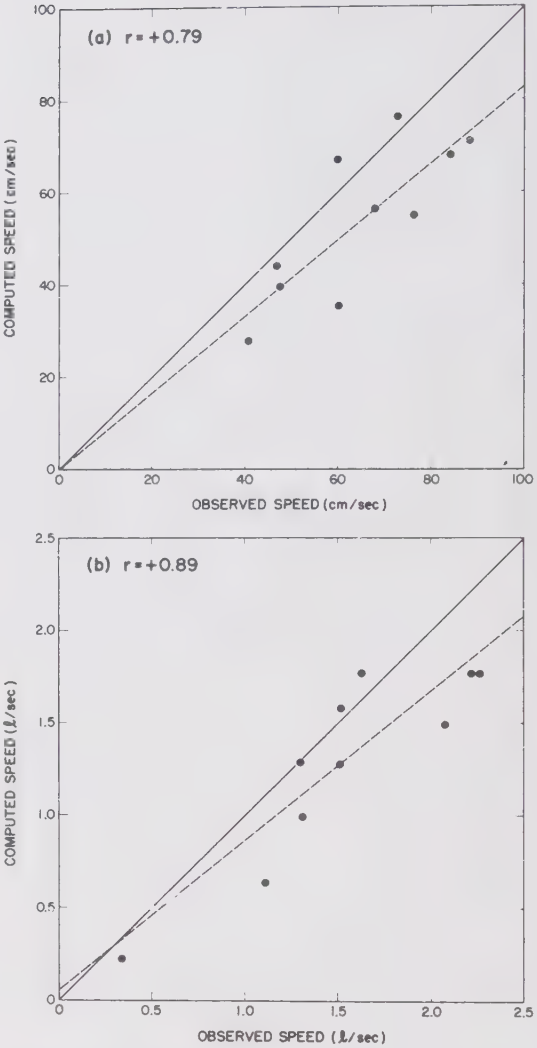

FIGURE 7.—Correlation between observed swimming speeds of scombroids and the computed minimum speed for hydrostatic equilibrium (a) in cm/sec, and (b) in body lengths/sec. Data from Table 3. Solid line shows expectation for perfect agreement and dashed line is the linear regression of expected speed on observed speed. Correlation coefficients, *r*, are given on graph.

(1966) as most efficient for migration by aquatic organisms.

Among the species with gas bladders, *T. albacares* and *T. obesus* have the largest pectorals, but *Ac. solandri* with small pectorals swims the slowest. The difference appears to be primarily from differences in gas bladder volume and resulting density. The large gas bladder and low density of *Ac. solandri* more than compensate for small pectoral fins.

At larger sizes all species swim slower in body lengths per second (Figure 8b), but owing to the allometric growth of the gas bladder, both large *T. albacares* and *T. obesus* can swim at slower speeds even in absolute units (centimeters per second). Their weights in water increase more slowly than their lifting areas after the fish attain approximately 50 cm FL.

A word of warning about Figure 8 is that the predicted speeds are extrapolated outside of the range for which morphometric and body density data were available. In addition, the density data for *Ac. solandri* was based only on animals 125 cm long. Likewise, the density data on *T. obesus* was limited.

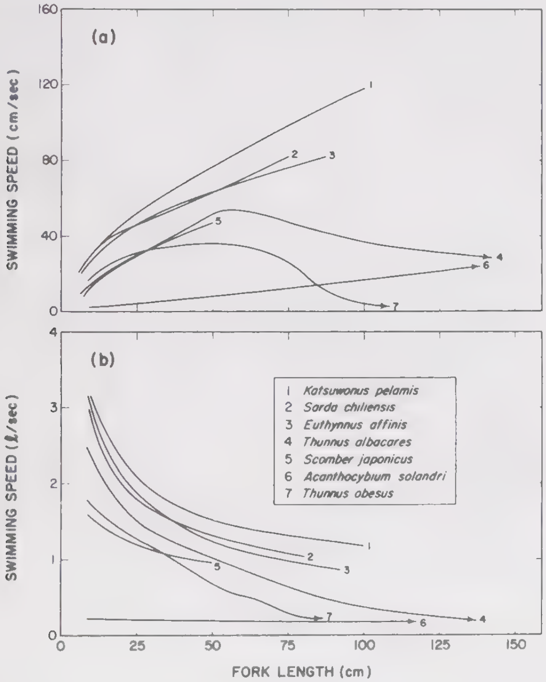

FIGURE 8.—Estimated minimum swimming speeds of seven scombroid fishes for maintaining hydrostatic equilibrium in (a) cm/sec and (b) body lengths/sec. Estimates from equation 1 and data in Table 4. See text for explanation.

OTHER FEATURES ASSOCIATED WITH BASAL SPEED

Scombroid fishes have many adaptations for efficient continued movement through the water. They have a high hemoglobin level (Klawe, Barrett, and Klawe, 1963), a large dark muscle (Kishinouye, 1923) for continuous locomotion (Rayner and Keenan, 1967), and a streamlined shape (Walters, 1962; Aleev, 1963; Alexander, 1967). The following analyses were to determine whether these adaptations were strongly associated with the basal or typical swimming speed. If differences in these characteristics varied closely with differences in typical speed, then I would argue that these adaptations were primarily selected for continuous slow swimming rather than maximum, burst speeds. Data on the burst or maximum speeds of these species are limited but do not indicate a strong association with typical speed. The burst speeds of 6-21 *l*/sec for *T. albacares* and 12-19 *l*/sec for *Ac. solandri* measured by Walters and Fierstine (1964) with a piscatometer at sea were approximately the same even though typical speed observed for *Ac. solandri* was less than one-fourth those of *T. albacares* (Table 3). Maximum speeds of four species measured photographically at sea or in shoreside tanks differ from species to species but not in relation to the typical speeds (Table 6).

TABLE 6.—Comparison of typical and maximum speeds observed from four scombroids.

Species	Speed (*l*/sec) Typical (Table 3)	Maximum	Source for maximum speeds
Thunnus albacares	1.3	10	Yuen (1966)
Sarda chiliensis	1.5	6.5	Magnuson and Prescott (1966)
Katsuwonus pelamis	1.5 1.6 2.2	14.4	Yuen (1966)
Euthynnus affinis	2.1	12.5	Walters (1966)

Dark muscle size was determined from dissections of fresh material—the difference in the coloration of the dark muscle and the rest of the muscle block was sufficiently visible that the entire dark muscle could be removed and weighed. Its size was expressed as a percentage of fish mass. Body shape was determined from dorsal and lateral photographs of fresh dead fish. The maximum body height (H) and maximum body width (W) as a percent of fork length were averaged to represent the maximum thickness ($\frac{H + W}{2}$) of the body. The position of maximum thickness along the length of the fish was expressed as percent of fork length. It was determined by averaging the measurements from both dorsal and lateral views. Usually the position of maximum height for a species was 1 to 3% (of fork length) more posterior than the position of maximum width.

Data on dark muscle, blood hemoglobin, maximum body thickness, and the longitudinal position of maximum body thickness are presented for seven scombroid species in order of decreasing typical swimming speeds in Table 7. The size of the dark muscle (Table 7) ranged from 1.8% of the body mass for *Ac. solandri*, 125 cm long, to 10.3% of body mass for *Au. rochei*, 31 cm long. Within single species, the relative size of the dark muscle is smaller for larger animals. For example, *T. obesus* approximately 55 cm long have a dark muscle 7.7% of the body mass, whereas those 125 cm long have a red muscle of 4% of the body mass. I observed the same trend but with different magnitudes for other species for which a wide range of lengths were examined. Blood hemoglobin ranged from 10.4 g/100 ml of blood for *Ac. solandri* to 19.2 g/100 ml for *Au. rochei* (Table 7). This range includes values comparable to mammals—man for example has ca. 15 g/100 ml.

Typical speeds were positively correlated (Figure 9) with dark muscle size ($r = +0.86$, $n = 9$, $P < 0.005$) and with blood hemoglobin ($r = +0.83$, $n = 9$, $P < 0.005$). Approximately 70% of the variation in both dark muscle size and hemoglobin concentration are associated with variation in typical speeds. The size of the dark muscle and the concentration of hemo-

TABLE 7.—Relative size of dark muscle, blood hemoglobin concentration, and body morphology of various scombroids for comparison with the typical swimming speeds. Dark muscle and body morphology from present study. Fish ordered by decreasing swimming speeds (l/sec).

			Dark muscle			Hemoglobin		Body morphology					
Species	Fork[1] length (cm)	Observed speed (l/sec)	(% M_f)	95% confidence interval on mean	n	(g/100 ml)	Source	Fork[2] length (cm)	n	H Maximum body height (% l)	W Maximum body width (% l)	$(H + W) \div 2$ Maximum thickness (% l)	Distance from snout to position of maximum thickness (% l)
Au. rochei	31	2.19	10.3	±0.4	7	19.2	Barrett and Williams (1965)	32- 37	10	24.3	17.4	20.8	40.2
K. pelamis	39	2.17	8.4	±0.2	15	16.7	Barrett and Connor (1962)	37- 43	9	25.4	17.8	21.6	43.0
E. affinis	36	2.11	8.1	±0.5	22	—	—	37- 43	7	27.2	18.0	22.6	40.4
K. pelamis	38	1.55	8.4	±0.2	15	16.7	Barrett and Connor (1962)	37- 43	9	25.4	17.8	21.6	43.0
Sa. chiliensis	57	1.54	6.2	±0.4	4	12.9	Barrett and Williams (1965)	45- 65	12	21.8	15.1	18.4	39.5
K. pelamis	48	1.49	7.5	±0.3	18	16.7	Barrett and Connor (1962)	44- 57	12	26.3	18.6	22.4	42.0
T. albacares	35	1.31	7.4	—	2	14.3	Barrett and Connor (1962)	28- 45	6	27.8	16.8	22.3	41.2
T. obesus	36	1.31	—	—	—	15.6	Barrett and Williams (1965)	46- 48	3	28.6	17.9	23.2	35.5
T. obesus	55	1.08	7.7	±0.6	13	15.6	Barrett and Williams (1965)	50- 60	13	28.7	18.5	23.6	37.5
Ac. solandri	125	0.33	1.8	±0.5	6	10.4	Barrett and Williams (1965)	123-130	6	14.6	10.4	12.5	37.3

[1] Lengths of fish observed for swimming speed. Dark muscle data for fish of approximately same lengths.
[2] Lengths for body morphology.

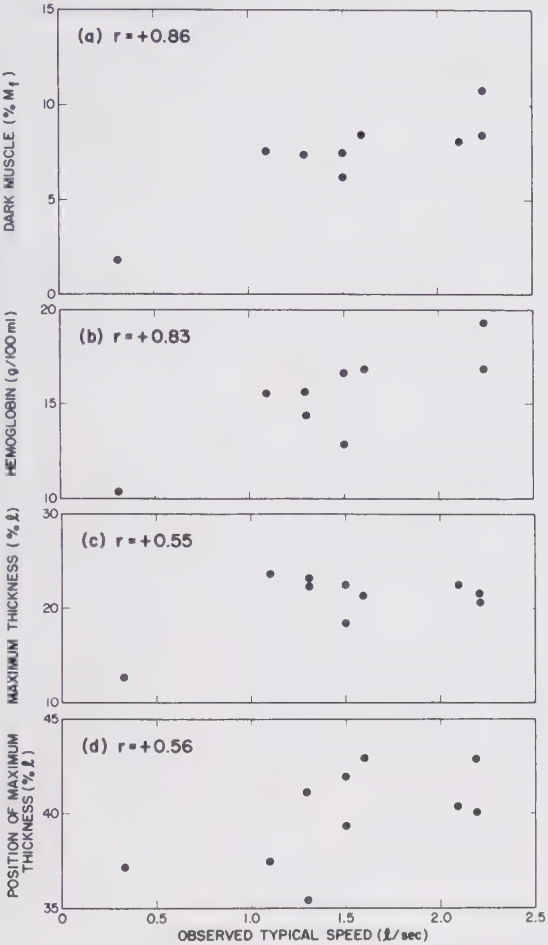

FIGURE 9.—Relation between observed swimming speeds and (a) the relative size of the dark muscle and (b) the concentration of blood hemoglobin, (c) maximum thickness of body, and (d) the position of maximum thickness along the length of the fish. Data from Table 7. Correlation coefficients, *r*, are given on graph.

globin are also highly correlated ($r = +0.82$, $n = 8$, $P < 0.005$). As expected, the dark muscle used for continuous slow speed is larger for species with faster typical swimming speeds. However, concentrations of blood hemoglobin also appear to be keyed to typical speeds and routine metabolism. Differences in need to transport oxygen sufficient for burst speeds apparently influenced hemoglobin levels little. Perhaps this is so because an oxygen debt can be temporarily incurred for burst activity.

Typical speeds in body lengths per second (Figure 9c, d) were also correlated with maximum thickness of the body ($r = +0.55$, $n = 10$, $P < 0.05$) and with the position of maximum thickness ($r = +0.56$, $n = 10$, $P < 0.05$). If speed is given in centimeters per second, the correlation +0.21 and +0.49 with maximum thickness and the position of maximum thickness are not statistically significant at $P < 0.05$.

Maximum thickness of the body ranged from 12.5 to 23.6% of fork length but only *Ac. solandri* had a value less than 18% (Table 7). Only 30% of the variability in thickness is associated with typical speeds. Thus, these variations do not appear to be closely related to differences in typical speeds (Figure 9c) with the exception that the species with the lowest typical speed, *Ac. solandri*, also had a low thickness ratio that would not be expected to minimize drag. Minimum drag should result from thickness ratios near 22% (Alexander, 1967). Differences among *Auxis*, *Katsuwonus*, *Sarda*, and *Thunnus* vary over a narrow range near 22% in a manner not related to typical swimming speeds.

Scombroids with faster typical speeds tend to have the thickest part of their body more posteriad (Figure 9d). Only 30% of this variation is associated with basal speed, but the trend is sensible in that the more laminar flow profiles should occur in the faster fishes.

In conclusion, all four characteristics, size of dark muscle, hemoglobin concentration, body thickness, and the position of the thickest part of the body are statistically related in a sensible manner to the variations in slow typical speeds of scombroids. The relations are poorer for the two characteristics involved in reducing drag, apparently because these features are more important at burst speeds than at typical speeds.

PROBLEMS ASSOCIATED WITH LARGE SIZE

Among the scombroid and xiphoid fishes, there is a great diversity in maximum body size, areas of pectoral fins, and the presence or size of the gas bladder. Data on these

TABLE 8.—Published data for scombroid and xiphoid fishes on maximum mass, the presence or absence of a gas bladder, and the relative length of pectoral fins. Species are ordered from smallest to largest known mass. Where only the length was known, mass was estimated from Figure 3 from a similarly shaped species.

Species	Maximum size			Gas bladder		Pectoral fins	
	Mass	Fork length	Source[1]	Present	Source[1]	Short (<20% FL) Long (≥20% FL)	Source[1]
	kg	*cm*					
Rastrelliger faughni	—	(20)	24	Yes	24	Short	24
Rastrelliger brachyosoma	—	(22)	19	Yes	24	Short	19
Rastrelliger kanagurta	—	(28)	19	Yes	24	Short	19
Cybiosarda elegans	1	—	6	No	10	Short	9
Scomberomorus multiradiatus	—	—	—	—	—	Short	10
Scomber japonicus	—	(35)	3	Yes	24	Short	9
Scomber australasicus	—	(45)	1	Yes	24	Short	24
Scomberomorus queenslandicus	2	(75)	6	—	—	Short	10
Scomberomorus sierra	2	(59)	7	—	—	Short	10
Scomberomorus koreanus	—	(60)	10	—	—	Short	10
Scomberomorus sinensis	—	(65)	10	—	—	Short	10
Scomberomorus guttatus	—	(82)	6	No	9	Short	9
Auxis rochei	—	(60)	6	No	9	Short	8
Scomberomorus concolor	—	(68)	10	No	9	Short	9
Sarda orientalis	3	—	20	No	13	Short	13
Scomber scombrus	3	—	3	No	24	Short	9
Auxis thazard	4	—	15	No	9	Short	41
Scomberomorus tritor	4	(98)	31	No	9	Short	9
Scomberomorus maculatus	5	—	2	No	9	Short	9
Euthynnus lineatus	5	—	5	No	12	Short	12
Sarda sarda	5	—	4	No	21	Short	9
Scomberomorus semifasciatus	—	(100)	25	No	9	Short	25
Scomberomorus niphonius	—	(101)	25	No	9	Short	25
Sarda chiliensis	—	(72)	16	No	12	Short	9
Scomberomorus lineolatus	6	—	18	No	40	Short	40
Grammatorcynus bicarinatus	11	—	36	Yes	36	Short	36
Orcynopsis unicolor	13	—	32	No	32	Short	9
Allothunnus fallai	14	—	6	No	35	Short	6
Thunnus atlanticus	16	—	17	Yes	11	Long	11
Scomberomorus regalis	16	—	3	No	9	Short	9
Euthynnus affinis	—	(100)	6	No	21	Both	41
Katsuwonus pelamis	22	—	6	No	39	Short	14
Euthynnus alleteratus	—	(122)	23	No	12	Short	12
Thunnus tonggol	27	—	6	No (rudimentary)	11	Both	11
Scomberomorus cavalla	37	—	4	No	10	Short	25
Thunnus maccoyii	—	(145)	11	Yes	11	Long	11
Thunnus alalunga	44	—	6	Yes	11	Long	11
Gasterochisma melampus	—	(165)	6	Yes	9	Short	22
Scomberomorus commerson	59	—	29	No	10	Short	25
Acanthocybium solandri	63	—	6	Yes	9	Short	9
Gymnosarda unicolor	80	—	21	Yes	21	Both	37
Tetrapterus pfluegeri	90	—	33	Yes	28	Both	33
Tetrapterus angustirostris	90	—	33	Yes	28	Short	34
Tetrapterus belone	90	—	33	Yes	33	Short	33
Istiophorus albicans	90	—	33	Yes	28	Short	33
Tetrapterus albidus	90	—	33	Yes	28	Both	33
Thunnus albacares	135	—	6	Yes	11	Long	11
Istiophorus platypterus	150	—	30	Yes	28	Short	27
Tetrapterus audax	180	—	33	Yes	28	Both	34
Thunnus obesus	198	—	6	Yes	11	Long	11
Xiphias gladius	536	—	27	Yes	26	Short	27
Makaira mazara (Jordan and Snyder)	—	(430)	27	—	—	Both	27
Makaira indica	700	—	30	Yes	28	Long	27
Thunnus thynnus	730	—	38	Yes	11	Both	11
Makaira nigricans	900	—	33	Yes	28	Both	34

[1] Abe and Takashima (1959).
[2] Beardsley and Richards (1970).
[3] Bigelow and Schroeder (1953).
[4] Breder (1948).
[5] Calkins and Klawe (1963).
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[12] Godsil (1954).
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[15] Gosline and Brock (1960).
[16] Hildebrand (1946).
[17] Idyll and de Sylva (1963).
[18] Jones and Silas (1962a).
[19] Jones and Silas (1962b).
[20] Kikawa (1963).
[21] Kishinouye (1923).
[22] Lahille (1905).
[23] Marchal (1963).
[24] Matsui (1967).
[25] Munro (1943).
[26] Nakamura et al. (1951).
[27] Nakamura, Iwai, and Matsubara (1968).
[28] Norman and Fraser (1948).
[29] Ogilby (1954).
[30] Osipov, Kizevetter and Zhuravlev (1964).
[31] Postel (1955).
[32] Postel (1956).
[33] Robins and de Sylva (1963).
[34] Royce (1957).
[35] Serventy (1948).
[36] Silas (1963a).
[37] Silas (1963b).
[38] Tiews (1963)
[39] Waldron (1963).
[40] Williams (1960).
[41] Williams (1963).

characters were surveyed from the literature and are presented in Table 8. To determine whether the hydrostatic requirements of swimming have had some influence on or interact with the maximum size, the occurrence of gas bladders and the occurrence of long pectoral fins were compared for small, medium, and large scombroid and xiphoid fishes (Table 9). The distinction between short and long fins was arbitrarily set at a pectoral length of 20% or more of body length at any point in the life history.

Larger species apparently require a gas bladder but smaller species do not. All of the 14 species $\geqslant$ 70 kg had gas bladders but only 26% of 19 species $\leqslant$ 6 kg had gas bladders (Table 9). Medium size fish, 7-69 kg, were intermediate. The largest species without a gas bladder was *Scomberomorus commerson* at 59 kg (Table 8). Apparently the presence of a gas bladder is obligatory for those species greater than 60 kg. The gas bladder overcomes some weight in water, reduces minimum required speeds, and results in a design that could reduce energy expenditures for the larger species.

The larger fishes also tend to have relatively longer pectoral fins. Of the 15 species $\geqslant$ 70 kg, 67% have long pectorals at some stage in their life history but none of the 25 species $\leqslant$ 6 kg ever have long pectorals (Table 9). Medium size fish, 7-69 kg, were intermediate.

The two adaptations that make slower speeds possible, large pectorals and a gas bladder, have some tendency to occur together. Of 24 species without a gas bladder, 92% (22 species) have short pectoral fins and of 25 species with a gas bladder only 48% (12 species) have short pectoral fins (Table 8). Apparently small species require neither large pectorals nor a gas bladder to have a required swimming speed slow enough to maintain. For these species, in most cases, the advantages of not having a gas bladder or the drag associated with large pectoral fins have overweighed the advantage of a slow required speed in the course of evolutionary history. Apparently large species have achieved speeds slow enough for a consistent overall design by the joint effects of pectorals and the presence of a gas bladder. For these species if the gas bladder were large enough, large pectorals were not necessary; but if the gas bladder were not large enough, selection occurred for large pectorals.

TABLE 9.—Occurrence of a gas bladder and the occurrence of long pectoral fins among scombroid and xiphoid fishes with different maximum masses. (A summary of Table 8.)

Item	Maximum mass (kg)						
	$\leqslant$6		7-69		70-900		Total
	No.	*%*	*No.*	*%*	*No.*	*%*	*No.*
Gas bladder:							
Present	5	26	6	40	14	100	25
Absent	14	74	9	60	0	0	23
Total	19	100	15	100	14	100	48
Pectoral fins:							
Long	0	0	5	33	10	67	15
Short	25	100	10	67	5	33	40
Total	25	100	15	100	15	100	55

Thus large species have a gas bladder and may or may not have long pectoral fins, while small species may or may not have a gas bladder and in neither case have long pectorals. In addition, large xiphoids with the large gas bladder may be able to use the pectoral for functions other than lift production. For example, the reduction of pelvic fins among xiphoids means that the pectorals must also produce any downward forces often ascribed to the pelvics.

The joint influences of maximum mass, body density, and lifting areas on minimum possible speeds give some perspective to the problem of large size (Figure 10). Surfaces of minimum swimming speeds were calculated for hypothetical 1-, 10-, and 100-kg scombroids with a lift coefficient of 1.0 for the pectoral fins. The keel was assumed to produce no lift. As expected, the smaller the gas bladder, that is, the greater $(D_f - D_e)$, the faster the fish must swim to maintain hydrostatic equilibrium. Also, the smaller the pectoral fins (A_{f_t}), the faster the fish must swim.

For small scombroids of 1 kg, changes in the density have little influence on required speed. And once the pectoral fins reach at least 50 cm^2, further increases in area have little influence on required speed. A 1-kg scombroid would be about 40 cm long. Fish this long

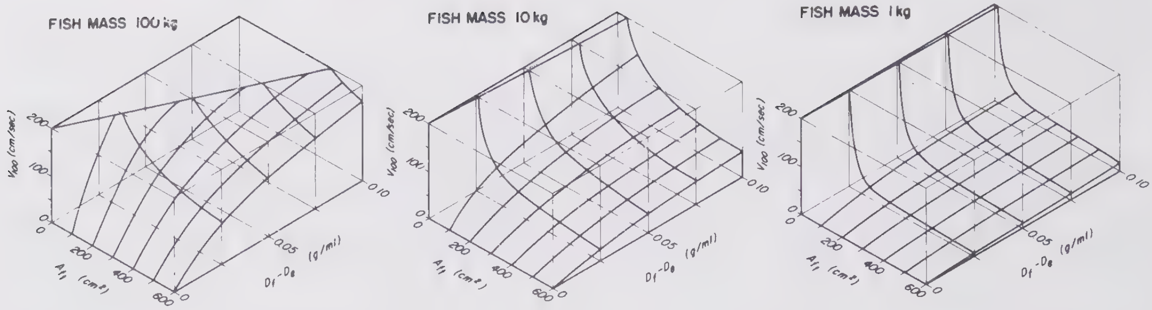

FIGURE 10.—Surfaces of minimum speeds required for hydrostatic equilibrium computed with different values of A_{f_t} and $(D_f - D_e)$ for hypothetical scombroids with a mass of 1, 10, or 100 kg. Speeds were computed from equation 1 with $\bar{C}_{L_f}$ set at 1.0 and D_e or ρ set at 1.025 g/ml.

should be able to maintain speeds near 100 cm/sec according to data from nonscombroids summarized in Figure 18 of Magnuson (1970). If there were some disadvantage to having a gas bladder, the loss of the bladder would not impose impossible levels of activity. Thus, the absence of a gas bladder and the occurrence of small pectorals among some small scombroids are consistent with the expectations of Figure 10 for 1-kg fish.

If hypothetical 10-kg and then 100-kg scombroids are considered (Figure 10), the presence of a gas bladder can be seen to be increasingly important to retain low levels of swimming activity. Required speed decreases rapidly with increasing pectoral size up to about 100 cm² for 10-kg fish and up to 200 cm² for 100-kg fish compared to 50 cm² for 1-kg fish. For a 100-kg fish and $(D_f - D_e) = 0.025$, as lifting areas increase from 200 to 700 cm², required speed declines to about 100 cm/sec. This constitutes a significant reduction in speed and helps explain why 100-kg *Thunnus* have pectoral lifting areas as great as 700 cm². Large scombroids could reduce energy expenditures with larger than expected pectoral fins.

Computed minimum speeds were slower than 40 cm/sec for a 100-kg *Thunnus* (Figure 8). If its pectoral fins were as small as those of *K. pelamis*, it would have to swim at least 90 cm/sec; and if it also had no gas bladder, its minimum speed would have to be 160 cm/sec.

Adaptations that serve to make low activity possible for large scombroids and xiphoids may reduce required speed well below the endurance speed or even below the most physiologically efficient speed for a species to migrate. No data on maximum endurance speeds are available for fish this large, but endurance speeds of sockeye salmon, *Oncorhynchus nerka*, in centimeters per second, increases as length increases (Brett, 1965). The relationship, speed $= 19\ l^{0.5}$, was determined from *O. nerka*, 8 to 54 cm FL, over periods only as long as 1 hr. Another data set (Hunter, 1971) for the jack mackerel, *Trachurus symmetricus*, is similar but based on shorter fish, 9-18 cm long, for longer periods, 6 hr. The relation was speed $= 22\ l^{0.6}$. Extrapolation of these relationships from a salmonid, 50 cm long, or a carangid, 18 cm long, to scombroids, about 80 and 180 cm long, seems a bit unrealistic, but if done indicates that the required speeds, even for a large hypothetical fish with short pectoral and no gas bladder, are considerably below the extrapolated endurance speeds. And a 100-cm *T. albacares* with its gas bladder and large pectorals swims at speeds less than one-sixth the extrapolated endurance speeds of a salmonid and less than one-fourth the speeds predicted by Shuleikin (1966) as most efficient for migration. Shuleikin's theoretical model was based on the speed at which the fish expended the least energy to overcome internal friction of muscles and external friction from movement through water.

Perhaps for the large fish the capability for low speed, makes possible speeds which are energetically prudent in an ecological sense.

Unfortunately the energy balances for these species are not known, especially in regard to energy expended for energy encountered as prey and in regard to energy conserved by low activity during times of day that feeding does not occur. However, in my view the most consistent explanation for the adaptations that reduce required speeds among larger scombroids and the xiphoids is that the speeds must be energetically prudent; and the larger the fish, the less likely this would be possible without a gas bladder and large lifting hydrofoils. Alternatively, but less likely in my opinion, perhaps Brett's and Hunter's estimates of endurance speeds and Shuleikin's estimate of the most efficient speed for migration are overestimates of the physiological capabilities of large scombroids and xiphoids for sustained swimming.

Larger scombroids are then not able to avail themselves of whatever advantages have been achieved by some smaller species and individuals of scombroids by the loss of a gas bladder. Problems of large size among scombroids become either the possibility of an energetically imprudent basal speed requirement to maintain hydrostatic equilibrium or a loss (Magnuson, 1966b; Aleev, 1969), owing to a large gas bladder, in vertical mobility especially near the sea surface. I have observed *K. pelamis*, a species without a gas bladder, swim vertically upward at burst speeds in the top 10 m of the sea. Large scombroids and xiphoids would be expected to live either (1) deep in the water column where rapid vertical excursions have little effect on gas expansion or (2) immediately below the surface and making no rapid upward excursions. The pressure change experienced in an ascent from 10 m to the surface results in a 100% increase in the volume of an unrestricted gas bladder but an ascent from 100 to 90 m results in an increase in volume of only 10%. Alternatively, (3) to retain rapid vertical mobility, those with gas bladders and living near the surface would require remarkably strong-walled gas bladders that could maintain the gas at greater than ambient pressures. A casual review of the natural history of large scombroids and xiphoids suggests that all three alternatives are evidenced in one form or the other. The most unlikely species would be one with a large, thin-walled gas bladder that also cruised at 10 m below the surface and chased its prey or escaped predation vertically toward the sea surface.

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Off the glorious Kona coast
of the Island of Hawaii, sportsmen
and scientists have gathered for
11 summers to study the habits
of the billfish.

Investigations of Billfish Biology at the Hawaiian International Billfish Tournament

JOHN J. NAUGHTON

ABSTRACT

Since 1962 the Southwest Fisheries Center's Honolulu Laboratory, National Marine Fisheries Service, has sent an investigating team to the annual Hawaiian International Billfish Tournament. There the team collected biological data for marine sport fisheries research. This paper outlines the tournament and NMFS participation and summarizes data collected there from 1962 to 1972. In order of abundance, billfish species taken by tournament anglers were Pacific blue marlin, Makaira nigricans; *striped marlin,* Tetrapturus audax; *black marlin,* M. indica; *sailfish,* Istiophorus platypterus; *and shortbill spearfish,* T. angustirostris. *Yellowfin tuna,* Thunnus albacares, *weighing 100 lb. or more also qualified and was the second most abundant game fish species taken. Results of investigations are discussed including marlin diet, sex ratio, sexual dimorphism, fishing effort, and marlin movements on the fishing grounds.*

INTRODUCTION

The Hawaiian International Billfish Tournament (HIBT) has been conducted off the west (Kona) coast of the island of Hawaii every summer since 1959. Beginning in 1962, the Southwest Fisheries Center's Honolulu Laboratory, National Marine Fisheries Service (NMFS), has sent an investigating team to each tournament to collect biological data from billfish taken by tournament anglers. This paper outlines the Honolulu Laboratory's participation in the tournament, describes the methods of collecting data, and presents a summary of these data.

THE TOURNAMENT

The HIBT is an 8-day event held each year during the summer months, usually July or August. Fishing is done for 5 days, Monday through Friday, from 8 a.m. to 5 p.m. Some 50 to 85 select foreign and U.S. teams participate, with Hawaiian teams comprising a large part of the U.S. representation. Each team consists of up to six members, with any four permitted to fish on a given day.

Trolling artificial lures at 5 to 8 knots or live bait at either very slow speeds or while drifting are the two methods of fishing allowed. International Game Fish Association rules are strictly adhered to. Fishing is done from individually owned or chartered trolling boats ranging in length from 16-ft outboards to 50-ft diesel powered sampans. Only fish caught on rod and reel qualify. Handlines are permitted solely for the catching of bait.

The fishing area extends the entire length of the west coast (Kona Coast) of the island of Hawaii. A grid system divides it into 26 different areas (Figure 1). All fish submitted for scoring are landed at the pier in Kailua-Kona and weighed on the official scale. Anglers fill out prize entry forms and exhibit the bait, rod, reel, gaff, and tackle with which their fish were caught, as well as furnish names of all witnesses.

Although the tournament is a billfish tournament, tuna weighing 100 lb. and over qualify. The yellowfin tuna, *Thunnus albacares*, is the predominant species of large tuna taken by trolling in Hawaiian waters and the only species weighing over 100 lb. recorded from the tournament catch.

Scoring in the HIBT is as follows:

1. Marlin competition is on a team basis.
2. Tuna competition is on an individual basis.
3. The basic award in both divisions is one point per pound.
4. There is a 30% bonus for marlin caught on 80-lb. test line.
5. There is a 100% bonus for marlin caught on 50-lb. test line.
6. There is a 100-point bonus for the largest marlin of the day.
7. There is a 100-point bonus for the largest marlin of the tournament.
8. Bonus points for the largest fish of the day and the tournament are awarded on the basis of the weight of the fish exclusive of any bonus points for line strength.
9. In the event of a tie for the biggest fish of the day or the tournament, bonus points will be divided evenly.
10. In case of a tie in points at the conclusion of the tournament in the billfish division, the team having

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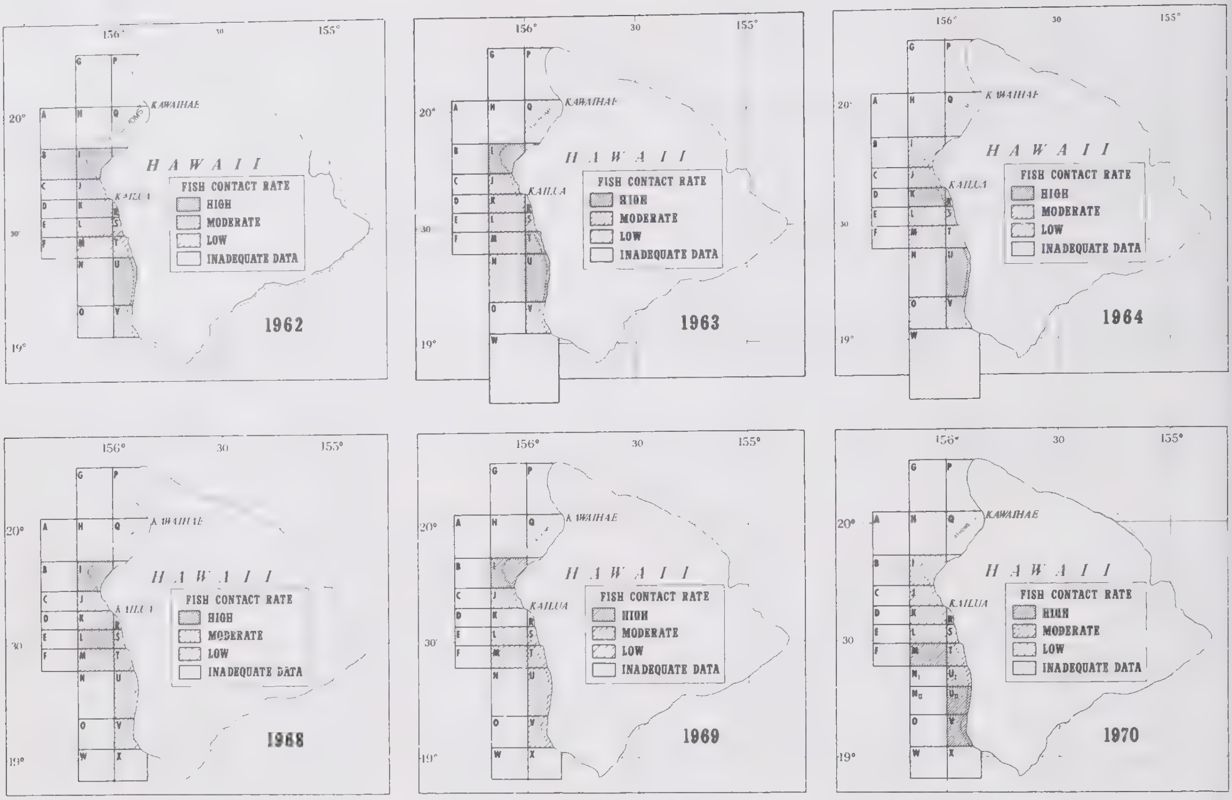

caught the largest fish of the tournament will be declared the winner.

PARTICIPATION BY THE NATIONAL MARINE FISHERIES SERVICE

At least one staff member from the Honolulu Laboratory, NMFS, is at the tournament each year in an official capacity as tournament biologist. Prior to each tournament he prepares a newsletter which is distributed to all participating anglers. It asks for their continued cooperation and outlines exactly what data will be collected at the tournament that particular year. The biologist sets up a display at tournament headquarters depicting fishery research activities carried out by the Honolulu Laboratory. He presents a talk at the pre-tournament briefing session for charter boat skippers and competitors, again going over what data will be collected and assuring anglers that no fish will be touched without the angler's permission.

During fishing days the biologist compiles fish contact and fishing effort data by monitoring the three daily radio reports transmitted to tournament headquarters by the fishing fleet. Tabulation of these data enables a fish contact rate chart to be compiled for each tournament (Figure 1).

After the fish are landed they are hoisted and weighed. At this time the biologist assists in the species identification. The fish are then transported to an observation area where the biologist takes morphometrics, dissects the fish for stomach content analysis, determines sex and condition of gonads, and carries out other specific sampling, e.g., collecting different tissues for determination of mercury content.

The weigh-in activities are of great interest to tourists and residents, and large crowds accumulate on the pier. Bleachers are set up for spectators, and an announcer describes weigh-in activities. The biologist periodically provides the announcer with the results of his examinations, such as the stomach contents and sex of each fish and other information of possible interest to the spectators. A variety of questions on billfish biology and fishery biology in general are often directed by the spectators to the biologist. The tournament participants themselves ask many questions of the same nature. The attending biologist must have therefore an up-to-date recall of basic as well as specific information concerning billfish and research programs of the Honolulu Laboratory.

Upon completion of the tournament

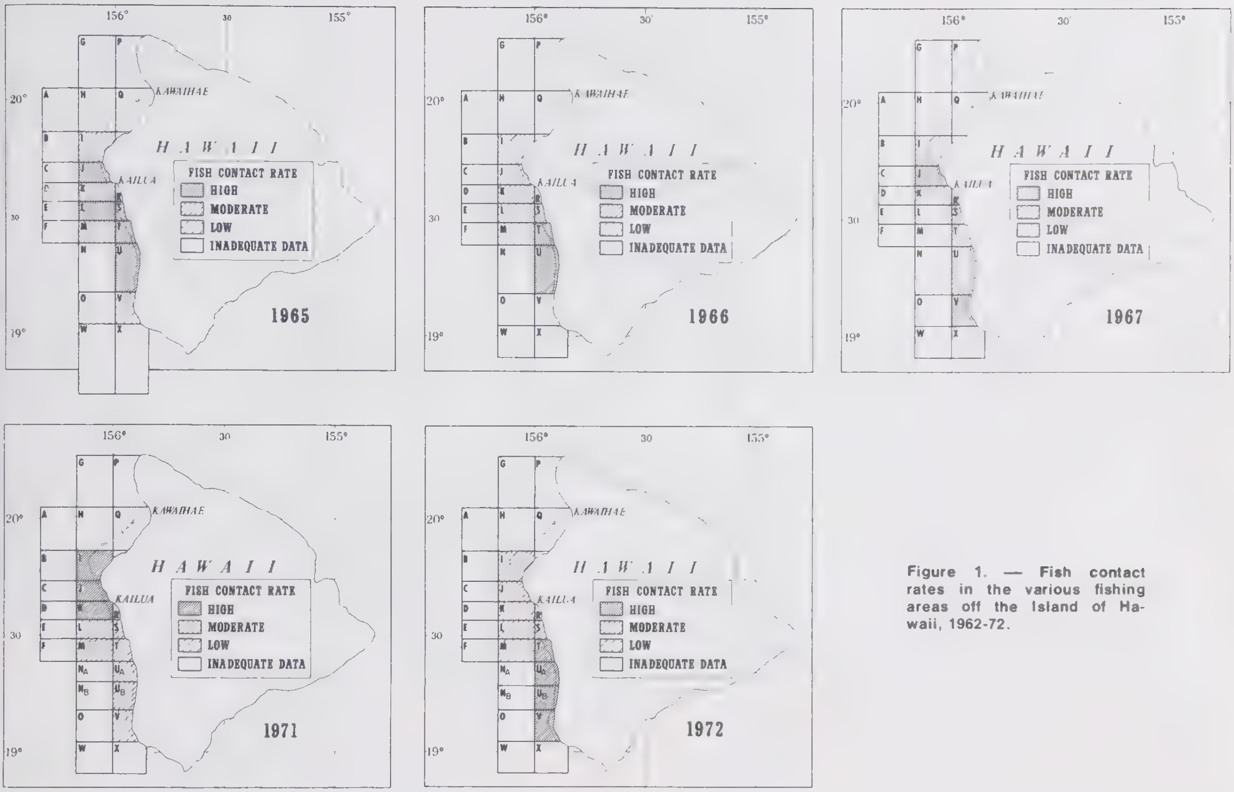

Figure 1. — Fish contact rates in the various fishing areas off the Island of Hawaii, 1962-72.

the biologist compiles a report.[1] describing the results of his investigations. This report is sent to all tournament participants, charter boat captains, and tournament staff.

During recent tournaments biologists on the Honolulu Laboratory's research vessel *Charles H. Gilbert*, working in conjunction with local charter boats, have been involved in tracking marlin for studies of their movements in Kona waters. The tags used in tracking are acoustic transmitters which are temperature sensitive. Thus, the water temperature around the fish may be determined by measuring the pulse rates. By combining this information with data on the temperature-depth profile of the water, the depth of the marlin can be determined.

Tracking is generally done during the week prior to the tournament. Once a marlin is hooked by the smaller, more maneuverable charter boat, the research vessel is contacted and alerted for tracking. As quickly and carefully as possible the marlin is brought alongside, where its condition is checked and its size estimated. If it appears to be in good condition the transmitter is attached to the dorsal surface of the marlin with a small anchor plate inserted just beneath the tough skin. The fish is released, and tracking begins.

In earlier tournaments large plastic drift panels were released in the fishing area by Honolulu Laboratory research vessels as part of a study of the surface currents off the Kona Coast. Whenever a panel was sighted by a tournament fishing boat its position was radioed back to headquarters. This enabled the NMFS biologist to plot the movements of the panels while they stayed on the fishing grounds. These experiments were carried out for five consecutive tournaments (1965-69) with excellent cooperation received from both charter boat captains and tournament anglers. Results confirmed the existence of a pair of large eddies in the fishing area, the northern one rotating counterclockwise and the southern rotating clockwise. Attempts to correlate fishing success with different features of these currents yielded no conclusive information; therefore, the drift panel experiments were terminated.

RESULT OF INVESTIGATIONS

The Catch

The total catches of qualifying game fish for the HIBT from 1962 to 1972 are documented in Table 1. For billfish, the Pacific blue marlin, *Makaira nigricans,* made up the greatest proportion of the catch (72.4%) with striped marlin, *Tetrapturus audax*, a poor second (2.1%). Black marlin, *M. indica* (1.3%), sailfish, *Istiophorus platypterus* (0.4%), and shortbill spearfish, *T. angustirostris* (0.2%) were taken rarely during the tournament. Because the blue marlin made up such a high percent of the tournament catch it is the only billfish species yielding sufficient data to discuss.

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[1] Report to participants of the Hawaiian International Billfish Tournament from 1962 to 1972. Mimeogr. Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, HI 96812

The abundance of blue marlin and lack of striped marlin taken during the tournaments is not surprising. Investigations of longline catches from Hawaiian waters clearly reveal a high catch rate for blue marlin during summer months and low catches during the winter (Strasburg, 1970). The reverse is true with striped marlin, which tend to be taken in large numbers when the blue marlin catch is lowest.

There are two possible factors to explain this segregation of species. The most probable is temperature. Striped marlin tend to live in cooler waters; therefore they move north in the summer (Howard and Ueyanagi, 1965), while the blue marlin possibly replace them from the south. Although trolling records are poor for year-round billfish catches in Hawaiian waters, personal observations indicate a substantial number of blue marlin taken by trolling even in the winter months. This tends to substantiate temperature as a major segregating factor, assuming those blue marlin that are still in Hawaiian waters remain in the warmer surface waters during winter and are therefore more susceptible to trolling and less to deep fishing longline gear.

Biologists John J. Naughton (left) and Robert T.B. Iversen examine stomach contents of fish caught at Hawaiian International Billfish Tournament.

Another factor which may explain this segregation is food supply. As discussed below, stomach contents of blue marlin caught during the tournament contain a high percentage of tuna, while striped marlin seem to prefer a variety of smaller fish, squid, and crustaceans. It has been shown that seasonal distribution of blue marlin and skipjack tuna, *Katsuwonus pelamis,* in Hawaiian waters coincide quite well (Strasburg, 1970). This would indicate that the appearance of large numbers of blue marlin may be related to the presence of one of their primary forage species.

It is not surprising that black marlin and sailfish are low in the tournament catches, since they are primarily found near continental land masses (Howard and Ueyanagi, 1965). Both are taken infrequently by local commercial longline vessels. The shortbill spearfish is rarely taken trolling although it is often seen in the local longline catches. This would indicate a subsurface existence for this species, at least in Hawaiian waters. The same is true for the swordfish, *Xiphias gladius*, which yields no record of having been taken by trolling in Hawaii, yet during late spring and early summer is common in local longline catches.

Yellowfin tuna weighing 100 lb. and greater is the second most abundant sport fish taken during the tournaments, as evidenced in Table 1 (23.6%). In fact, in 1971 it was the most abundant species in the catch. Generally these large yellowfin are more commonly caught by trolling in Hawaii during the summer months when the tournament is held. However, they can be taken year-round with spectacular runs developing at any time.

Table 1. — Numbers of qualifying game fish landed and teams fishing during Hawaiian International Billfish Tournaments, 1962-72.

Year	Blue marlin	Black marlin	Striped marlin	Shortbill spearfish	Sailfish	Yellowfin tuna ≥ 100 lb.	Total qualifying fish	Number of teams	Number of boat days fishing per fish
1962	30	1	—	—	1	19	51	68	6.7
1963	19	2	1	—	—	26	48	72	7.5
1964	31	—	1	—	—	2	34	69	10.1
1965	47	—	—	—	—	9	56	78	6.9
1966	26	3	2	—	—	7	38	72	9.5
1967	63	—	1	—	—	18	82	68	4.2
1968	36	2	4	—	—	4	46	85	9.2
1969	32	1	—	—	—	4	37	75	10.1
1970	91	—	2	—	2	14	109	73	3.3
1971	41	—	3	1	—	47	92	77	3.4
1972	77	—	—	—	—	11	88	59	3.4
Total	493	9	14	1	3	161	681	72*	6.8*
Percent of catch	72.4	1.3	2.1	0.2	0.4	23.6	100		

*Average.

Marlin Diet

Although billfish show great variations in dietary trends between different species as well as among separate populations of the same species (Strasburg, 1970), they are often quite consistent in their diets from any one area. The blue marlin stomach contents examined at the tournaments match contents of blue marlin caught on local longline, in that smaller scombrids (skipjack, yellowfin, kawakawa, *Euthynnus affinis*, and albacore, *Thunnus alalunga*), carangids, and squid predominate. During some tournaments, however, a sudden change occurs in their diet when an influx of uncommon forage items appears on the fishing grounds. As an example, during the 1972 tournament (Table 2), the young of a goatfish, *Mulloidichthys* sp., and a species of spiny puffer, Diodontidae, obviously became important food items, ranking comparably with the more conventional blue marlin food. It would appear, therefore, that blue marlin in Hawaiian waters feed on whatever forage species are available.

Some of the more unusual stomach contents from tournament-caught blue marlin have included juvenile billfish (including swordfish), deepwater lancetfish (Alepisauridae), and a 63-lb. bigeye tuna, *T. obesus*, found in the stomach of a 748-lb. blue marlin. The occurrence of deepwater lancetfish in very fresh condition indicates that blue marlin may be feeding at considerable depths during the day.

The few striped marlin from the tournament that have been examined usually contain pelagic stages of reef fish, squid, and crustaceans in their stomachs. Invariably the angler who takes an unusual billfish species (sailfish or shortbill spearfish) wants it mounted for a trophy; therefore, they rarely are dissected.

Table 2. — Stomach contents of blue marlin, *Makaira nigricans*, from Hawaiian International Billfish Tournament, 1972.

Food items		Day and number of stomachs containing listed food items					Percentage of occurrence
		August					
		7	8	9	10	11	
Fish							
Tuna	Scombridae						
Skipjack	*Katsuwonus pelamis*	—	—	—	1	1	3
Kawakawa	*Euthynnus affinis*	—	—	—	1	—	1
Unidentified		2	7	9	5	5	39
Mahimahi	Coryphaenidae	—	—	4	—	4	11
Jacks	Carangidae						
Opelu	*Decapterus pinnulatus*	—	2	2	1	3	11
Unidentified		1	—	—	—	1	3
Lancetfish	Alepisauridae	—	—	—	1	1	3
Goatfish	Mullidae						
Oama	*Mulloidichthys* sp.	2	3	2	4	4	21
Cardinalfish	Apogonidae	—	—	—	1	—	1
Squirrelfish	Holocentridae	—	—	2	1	—	4
Surgeonfish	Acanthuridae	—	—	—	—	1	1
Bonnetmouth	Emmelichthyidae	1	—	—	—	—	1
Pelagic spiny puffer	Diodontidae	3	6	7	2	4	31
Puffer	Tetraodontidae	—	1	—	—	—	1
Unidentified fish							
Large >12 inches		—	—	2	2	—	6
Small <12 inches		1	2	7	4	3	24
Invertebrates							
Squid	Decapoda	1	8	9	4	6	39
Empty or everted stomachs		3	2	1	5	2	18
Number of blue marlin examined Total: 72		11	17	17	17	10	—

Sex Ratio and Sexual Dimorphism

An unusual phenomenon noted from blue marlin catches in the tournament is the high ratio of males to females (Table 3). A random sample of 694 blue marlin from the Hawaiian longline catch consisted of 334 males and 360 females (Strasburg, 1970). Only during the 1964 tournament, however, did the sex ratio approach this expected 1:1 condition. It would seem that during the other 10 tournaments the blue marlin were segregated by sex on the fishing grounds.

Tournaments which produced the highest numbers of blue marlin (1965, 1967, 1970, 1972) also revealed the largest male to female ratios (4.4:1, 3.9:1, 4.5:1, and 8.0:1, respectively). The 8:1 ratio from the 1972 tournament catch is especially noteworthy. The unusual abundance of male blue marlin during these years was a major factor contributing to the success of those particular tournaments. Whether this surplus of males is due to fishing gear selectivity, a feature of reproduction or feeding behavior, or some other unknown factor is not yet known.

The weights of the 493 blue marlin caught in the tournaments from 1962 to 1972 ranged from 48 to 809 lb. Males ranged from 48 to 377 lb. whereas females were from 96 to 809 lb. Blue marlin, as well as black marlin, are known for their marked sexual dimorphism, with females attaining a much larger size (Royce, 1957). A general rule is that a blue marlin heavier than 300 lb. is a female. Of the 340 males taken during the tournaments only three were over 300 lb., weighing 309, 314, and 377 lb. each.

Table 3. — Sex ratios for blue marlin, *Makaira nigricans*, examined from Hawaiian International Billfish Tournaments, 1962-72.

Year	Number of males	Number of females	Ratio males to females
1962	16	7	2.3:1
1963	13	6	2.2:1
1964	14	12	1.2:1
1965	35	8	4.4:1
1966	16	8	2.0:1
1967	51	13	3.9:1
1968	24	10	2.4:1
1969	23	8	2.9:1
1970	63	14	4.5:1
1971	21	9	2.3:1
1972	64	8	8.0:1
Total	340	103	3.3:1*

*Average

Fishing Effort

Team radio reports are given at 10 a.m., 12 noon, and 3 p.m. Each team reports fishing areas and time spent in each, number of strikes, hookups, or boated fish since the last report, and the area of its reported fish contacts. Fishing effort is measured by fish contact per boat hour by fishing area. Each fish contact is counted only once as either a strike, hook-up, or boated fish. Allowance is made for the different lengths of the reporting periods and for the varying number of boats in each period and area. Only those areas in which five or more boats fished for one or more reporting periods are assigned a final rating.

The distribution of fish contact rates by fishing area for the 1962 to 1972 tournaments is shown in Figure 1. Often areas that produced the greatest catches did not necessarily have the highest fish contact rates. For example, area I produced the most blue marlin in 1972, but in final tabulation it only warranted a moderate contact rating (Figure I). This indicates that fishing effort was more intense in I, but that if the same boats had ventured south during the tournament to areas T, U_A, U_B, or V, their chances of taking a fish would have been better.

The last column in Table 1 summarizes fishing effort for the HIBT from 1962 to 1972. When number of boat days fishing per fish landed are considered, the 1967, 1970, 1971, and 1972 tournaments are all well below the average of 6.8 boat days per fish. As mentioned previously an influx of male blue marlin appears to be responsible for the success of three of these four tournaments. The exception, the 1971 tournament, was successful because of a tremendous run of large yellowfin tuna that year.

Another factor which perhaps contributed to the success of these tournaments was tidal phase. The NMFS biologists have been plotting fish contact rates against tidal cycle for most of the tournaments. Early observers noted from these data a suggestion that fishing for the most part was better during a rising tide with maximum range, such as that associated with a new moon. These observations were confirmed by charter boat captains and several tournament staff members. Because of this, recent tournaments have been scheduled to coincide with this feature of the tidal cycle, and, as can be seen from Table 1, the last three tournaments have been most successful.

Marlin Movements on Fishing Grounds

One week prior to the 1971 and 1972 tournaments five blue marlin were tagged with sonic tags and tracked: one during July 14-15, 1971 and four between July 25 and 28, 1972. Following is a summary of these tracking experiments from Yuen (in press). The first tagged marlin was tracked for 22 hr and 25 min before a malfunction in the tracking equipment forced a halt (Figure 2). This fish was a blue marlin estimated to weigh 600 lb. The second marlin was in doubtful condition when released and was difficult to track. Contact was lost after an hour. The third fish was tracked for 5 hr and 22 min before it was lost owing to a tactical error. The fourth marlin was abandoned after 7 hr when it remained stationary on the bottom soon after it was tagged, indicating that in all probability it had died. After 2 hr of swimming, the fifth marlin also went to the bottom.

Several features stand out from the marlin tracking studies. All viable marlin showed indication of staying above precipitous bottom, in this case between the 100- and 1,000-fathom isobaths. Although usually well above these depths, they apparently could sense some feature of the rapidly sloping escarpments far beneath them. The viable marlin also all moved in a northerly direction when released. From the drift panel studies it was determined that the current system west of the northern half of the island of Hawaii forms a counterclockwise eddy during the summer months with the inshore portion flowing northward. All marlin tracked appeared to be in this current system, and the fact that they moved north suggests the possibility that blue marlin orient or swim with currents. Swimming depths were quite different among the marlin tracked, ranging from the surface to 185 m. Vertical movements showed no pattern that could be related to time of day.

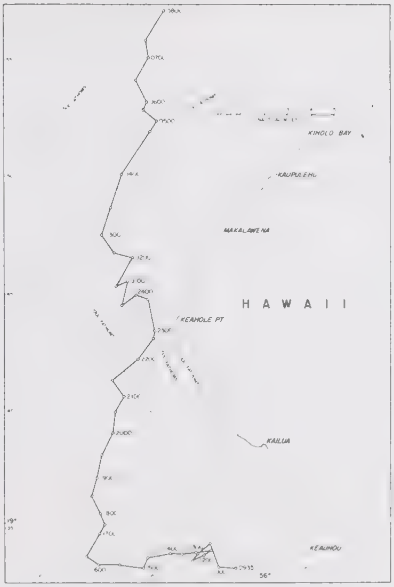

Figure 2. — Track of tagged Pacific blue marlin (ca. 600 lb.) during July 14-15, 1971. Positions on track taken at half-hour intervals.

CONTINUED INVESTIGATIONS

The HIBT has a long history of sports fisherman-scientist cooperation. This was highlighted by the unique International Billfish Symposium held to coincide with the 1972 tournament (Anonymous, 1972). Because relatively little is known concerning the status of billfish, both from a commercial as well as a sport fishing point of view, it is important to monitor these periods of intensive sampling that occur during tournaments. A substantial number of billfish tournaments are held throughout the world every year. It would be helpful if scientific investigations could be carried out at each tournament on a continuing basis.

ACKNOWLEDGMENT

I would like to thank Mr. Peter Fithian and the other members of the Board of Governors, HIBT, for their continuing cooperation in helping us collect data at the tournaments. I am also indebted to the charter boat captains and tournament anglers who provide fishing statistics and allow us to examine their catches.

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The Effect of Particles on Light Scattering in the Sea*

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Abstract: Relationships of light scattering to particle concentration and size distribution were experimentally determined to follow theoretical findings, both in laboratory suspensions and in a variety of conditions in the natural marine environment. Confirmation was obtained by electronic particle counts paired with scattering measurements that light scattering provides a measure of concentration of particle cross-section in the sea. The use of light scattering as a measure of particle bulk concentration is shown to require constancy of the distribution of particle size, which is met under prescribed circumstances in the upper part of the sea. A simple test can indicate the constancy of the size distribution. A tentative estimate is made of the effect particles have on the inherent properties of open ocean water.

1. Introduction

Although interactions between light and particle ensembles have stirred interest in a wide variety of the physical and biological sciences, light scattering measurements coupled with determination of particle characteristics in the sea have been limited. In particular, work on size and character of optically active particles has been restricted by the ephemeral nature of marine particles and by the lack of non-interfering methods of measurement. Recent refinements of electronic counting have been made possible limited work at sea on particle size distributions but there is still no direct *in situ* method available. Optical methods, on the other hand, offer the possibility of non-interfering, *in situ* measurement of some aspects of particle incidence in the sea. The purpose of this work is to derive through physically and oceanographically defined measurements the relationship of light scattering to size distribution and concentration of natural ensembles of particles and to specify conditions under which light scattering can be used to measure particle concentration.

A few investigators who have worked with both optics and particle characteristics (JERLOV, 1955; PICKARD and GIOVANDO, 1960; OCHAKOVSKY, 1966; TUCKER *et al.*, 1969; BEARDSLEY *et al.*, 1970; CARDER, 1970; CARDER *et al.*, 1971; PAK *et al.*, 1971) reach conflicting conclusions on the optical predominance of particle size classes. Of these, only OCHAKOVSKY combined optical measurements (volume attenuation rather than scattering) with bulk measures of particle load as well as size distribution measurements.

2. Theory and assumptions

The volume scattering function and its integral, the volume scattering coefficient, comprise one of the three inherent optical properties of water, the others being the volume absorption and volume attenuation coefficients.

Nearly every observation of light scattering in natural waters suggests control by particles of refractive index close to that of water and of dimensions large compared to the scattered wavelengths: the scattered light exhibits an intense forward component and independence of wavelength over much of the visible spectrum. VAN DE HULST (1957) who has summarized scattering theory in his classic reference work, refers to scattering from particles with these characteristics as "anomalous diffraction." The character of equations derived by VAN DE HULST from the MIE (1908) solution for scattering of a monochromatic plane wave incident on a homogeneous, isotropic sphere shows that

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the low scattering efficiency of particles below about 0.5 μm radius renders them optically ineffective at refractive index of 1.1 and measurement wavelength of 500 nm. Theoretical and experimental work by PENNDORF (1953), HODKINSON (1963), and HOLLAND and GAGNE (1970) shows that for polydispersed suspensions of large particles the optical cross section is directly related to geometric cross-section, even for irregularly-shaped particles oriented at random. This suggests that an effective area coefficient can be applied to measurements on natural particle ensembles.

For any given distribution of particle size, the area coefficient for the particle ensemble, $\bar{Q}$, takes on a constant value and may be taken outside the integral to be used as a bulk coefficient. The equation relating scattering to particle cross-section then becomes

$$s=\bar{Q}\int_0^\infty N\pi r^2\, dr \qquad (1)$$

Under polydisperse conditions $\bar{Q}$ is dependent only on changes in refractive index and on changes of the size distribution below particle radii of about 2 μm under normal measurement conditions.

The same argument can be used to justify the substitution of a composite or "effective" index of refraction for the individual index when particles having a variety of indices are under consideration, provided that such an effective index does not vary with particle size. Although some previous results are consistent with an increase in composite refractive index with depth in the sea over a large depth range (BURT, 1958; PAK *et al.*, 1971), the restricted depth range used in the present work (0 to 100 m) is unlikely to span any significant range of refractive index values. Further, the work was mainly conducted offshore where more constant proportions of materials of differing origin diminishes the effect of refractive index on variation of scattering.

The refractive index of individual components of natural particle ensembles may not vary widely in the sea. BURT (1952) indicated that the relative indices of both organic and inorganic materials of Chesapeake Bay water clustered closely around 1.15. While natural particles can have relative indices varying from 1.0 to 1.4 (JERLOV, 1968), the relative index for mineral substances has been estimated at a constant 1.17 by PAVLOV and GRECHUSHNIKOV (1966) and that of biological materials ranges rather narrowly between 1.03 and 1.06 for bacteria, plant and yeast cells (WYATT, 1968; LATIMER *et al.*, 1968; BRYANT *et al.*, 1969) and 1.10 for spores (LEWIS and LOTHIAN, 1954).

It seems clear from these considerations that the effect on light scattering from particle concentration and size distribution will be greater than the effect of variations of the composite refractive index over the restricted depth interval considered here. On this basis, the composite refractive index of particles under consideration is here assumed to be close to that of sea water and constant over the water masses where measurements were made.

The volume scattering coefficient s, defined in terms of particle ensemble characteristics by Equation (1), can also be defined optically summation of the scattered fluxes in every direction (4π steradians) from the irradiated volume containing the particle ensemble:

$$s=\int_0^{4\pi}\sigma(\theta)d\Omega$$

The term $\sigma(\theta)$ is the volume scattering function, defined by the equation

$$\sigma(\theta)=\frac{I_e(\theta)}{E_eV}$$

where $I_e(\theta)$ is the intensity of scattered light the direction θ, E_e is the irradiance on the scattering element of volume V. The volume scattering function thus describes the flux scattered through a unit solid angle Ω in the direction θ per unit of incident irradiance, per unit of incident irradiance, per unit volume of the scattering element.

The constancy of the slope of the forward part of the volume scattering function and the absence of extremums of the function in the upper layers of the sea has become apparent through the work summarized by DUNTLEY (1963), and through individual investigations of JERLOV (1961), HINZPETER (1962), SASAKI *et al.* (1960), OCHAKOVSKY (1966), and SPILHAUS (1968). These suggest that scattering at any of a wide range of forward angles can be specified from that at a single angle, and that the total volume scattering coefficient, s, can be similarly approximated. The latter has been started as a hypothesis by JERLOV (1951) and suggested by the results of a number of studies (JERLOV, 1961; TYLER, 1961; HISHIDA, 1966). Until recently the scarcity of adequate scattering data for the important extreme foward angles in sea water had not permitted a test of the hypothesis. SPILHAUS (1968), using observations from 30° to 130° estimated that the partial scattering coefficient over that interval could be estimated by $\sigma(45°)$ or $\sigma(30°)$ with less than 6 % error. MORRISON (1970a, b) has supplied the necessary data at extreme forward angles to provide a test of the adequacy of representing s by measurement at a singe forward angle. Using a co-axial scattering meter based on the experimental design used by DUNTLEY (1963) in a New Hampshire lake, MORRISON (1970a, b) measured scatterance at 0.20°, 0.62, and 1.26° and, with another instrument, from 25° to 140°. His test of the hypothesis confirms that of SPILHAUS (1968): very high correlation coefficients of the regression of s on $\sigma(30°)$ or on $\sigma(45°)$, both greater than 0.97, indicate the adequacy of representing s by any value of $\sigma(\theta)$ for the range $20° \leq \theta \leq 60°$.

The shape of Morrison's $\sigma(\theta)$ function is substantially that given by DUNTLEY (1963) who combined his own low angle lake data with that of KOZLYANINOV (1957) from the East China Sea. Because the integrated function (yielding s) frequently was much larger than expected from Morrison's independent estimates of volume absorption and attenuation, however, the exact relationship between s and $\sigma(\theta)$ at a given value of θ still cannot be specified even though the relationship was shown to be close.

Through theoretical considerations and the substantiating observations noted above, the following assumptions and simplifications can be made to validate light scattering as a measure of particle cross-section concentration.

That single scattering only need be considered in the sea over path lengths of less than 1 m and that scattering effects are additive.

That an area coefficient $\bar{Q}$ relating particle area to light scattering can be considered a constant.

That particles having irregular shapes scatter as spheres having the same cross-section and equivalent radius or volume.

That a constant, composite value of relative refractive index can be assigned to particle ensembles in the upper layers of the sea.

That scattering at a given forward angle represents total scattering, and hence concentration of particle cross-section as well.

3. Scattering by experimental suspensions

Because the scattering measurement is potentially diagnostic of particle size distribution and of particle concentration, laboratory experiments were conducted to separate these two variables as well as to confirm by observation and extend to other angles Deirmendjian's (1963) derivation from theory that scattering at $\theta = 45°$ is directly proportional to the particle cross-section concentration of polydispersed ensembles. Cross-section concentration is the combined expression of size distribution and volume concentration. It was to be hoped that the light scattering meter would be sensitive to both parameters the range of environmental variations to be encountered.

Aqueous suspensions were required in which particle size distribution could be varied while maintaining a constant value of particle concentration, and in which concentration could be varied without changing size distribution. Controlled artificial suspensions were suggested because size distribution, if not concentration, would have been difficult to manipulate using natural water suspensions. An additional requirement was that these suspensions be optically polydispersed *i.e.*, that a sufficient range of size present in such quantities as to produce a smooth, monotonic scattering function. If particle size fractions were to be changed to satisfy the separation of volume and projected area variables, it would also be necessary that Mie lobes, produced by scattering from monodisperse suspensions, be absent because the scattering signal at a given angle would otherwise depend more on the projected area of one size fraction than on that of the ensemble.

These requirements were met through the use of polystyrene latex sphere suspensions. The spheres are of nearly uniform, single sizes and are commercially available (Dow Chemical Corp.) Their uniformity facilitates analysis of concentration because only numbers per unit volume of suspension need be assessed.

Stock suspensions were made up for each of five sphere sizes (1.10, 1.86, 5.13, 7.25, and 15.95 μm diameter) by dilution of the original concentrate with filtered, deionized water. This size range was intended to provide sufficient polydispersion, when combined, to satisfy the optical requirement stated above. Aliquots of these stocks were analyzed in a Coulter equipped with a 30 μm-diameter office. Counts obtained were converted to volume concentration and to concentration of projected area.

Given those stock concentrations, combinations were made to yield four working suspensions having equal volumes of particles with as wide a variety of total particle cross-sections as possible while maintaining polydispersion. The working suspensions were then used to determine the response of the σ-meter to variation in particle cross-section.

The working suspensions each contained a volume concentration of 32.01×10^3 $\mu m^3/cm^3$ and projected area concentrations of 15.87×10^3, 10.37×10^3, 8.03×10^3, and 5.65×10^3 $\mu m^2/cm^3$. Polydispersion was enhanced because particle counts indicated that some of the latex spheres were in doublet and triplet form; these were accounted for in the calculations for preparation of the working suspensions.

The working suspensions were submitted within a short time after their preparation to the same light scattering meter, referred to as the σ-meter, as was used at sea. The σ-meter (described in the next section), which measures at 20° off the forward axis, was fitted with a closed cuvette to contain the suspensions.

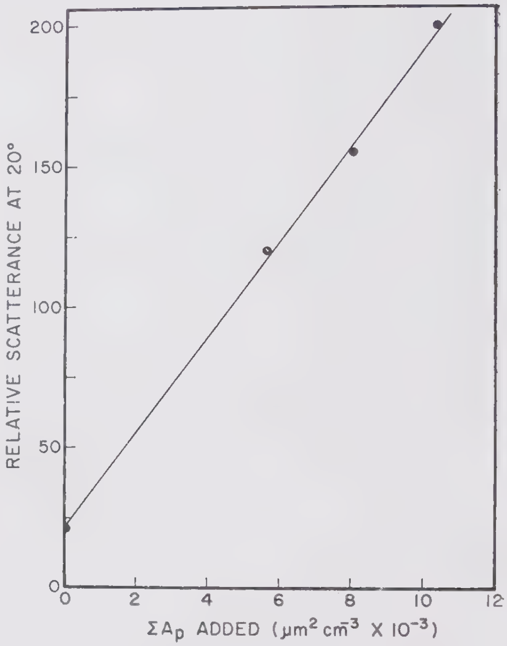

Fig. 1. Response of the σ-meter to variation of particle cross-section concentration at constant particle volume concentration.

Previous use of the cuvette showed that stray light was not detectable, as both projector and receiver were aimed into blind light traps beyond the sensed volume element of the projector beam. The σ-meter was standardized and operated in the same way in the laboratory as at sea. Results of these determinations are shown in Figure 1.

The suspensions were also submitted to a general-angle laboratory scattermeter made available by the Visibility Laboratory, Scripps Institution of Oceanography, which was capable of measurement at angles from 12-1/2° to 160° off the beam axis. The optical geometry of this instrument is not very well defined, due in part to the uncertain optical quality of the beaker used to contain the sample, through which the instrument must both illuminate and sense the volume element. The filter combination used resulted in a spectral sensitivity approximately equivalent to that of the σ(20°) meter. These measurements were made at 5° intervals from 15° off the forward axis of the beam to 100° to check the smoothness of the scattering function, *i.e.*, to check that no pronounced Mie lobes were present which would vitiate the test of scattering response to particle cross-section.

Results of these measurements, shown in Figure 2, indicate that no pronounced Mie lobes were present in the suspensions—maximums and minimums were not detected. There was, however, a change in the slope of the $\sigma(\theta)$ function that shows that the dispersion of particle sizes was not broad enough to generate a perfectly smooth function. These may be seen to be approximately equivalent for each of the suspensions so that the test of this hypothesis remains valid.

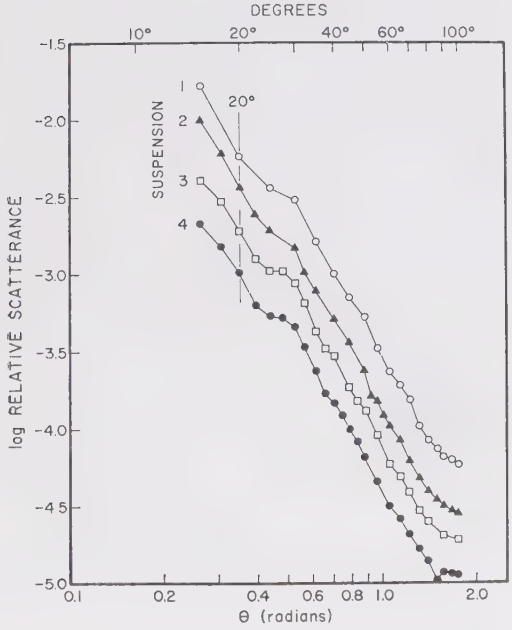

Fig. 2. Light scattering function for each of four known polydispersed suspensions. Suspensions 1 to 4 respectively contained 15.87×10^3, 10.37×10^3, 8.03×10^3 and 5.65×10^3 μm^2 of particles per cm^3 of suspension.

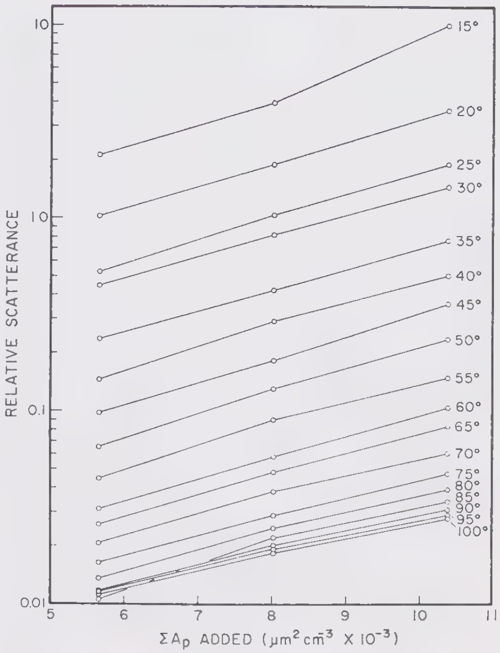

Fig. 3. Light scatterance as a function of particle cross-section concentration at angles shown.

Plots of scatterance at various measured angles are shown in Figure 3 as a function of particle cross-section. At most angles the relationship is linear and slopes are equivalent within instrument error despite the change in slope noted above. One of the working suspensions (containing $15.87 \times 10^3 \mu m^2/cm^3$) was subsequently found to have become contaminated by rod-shaped bacteria. Data for this suspension consequently were discarded although its scattering function is shown in Figure 2 as suspension 1.

This determination of the effect of total particle cross-section on scattering constitutes a test of the CLEWELL (1941) hypothesis that at constant mass (or volume) concentration, scattering from suspensions of particles large compared to the scattered wavelength will be directly proportional to the equivalent reciprocal diameter of the particle ensemble. The linear relationship observed between scattering at 20° (as well as at other angles) and total particle cross-section at constant particle volume constitutes confirmation of the hypothesis, as this is equivalent to the reciprocal diameter relationship.

The determination also expands Kalle's (1939) hypothesis, and Deirmendjian's (1963) derivation from scattering theory which state that scattering at 45° is directly proportional to particle cross-section concentration. Direct proportionality at other angles, including 20°, also occurs wherever polydispersed suspensions cause the scattering.

The concentrations of particle cross-section in the working suspensions used in these tests were three to 10 times more dilute than those observed at sea over a comparable range of particle sizes (OWEN, 1972). These latter concentrations will not give rise to appreciable multiple scattering, however, and it is therefore apparent that the laboratory results apply also to field measurements. The conclusion may be drawn that the scattering measurement is sensitive to environmental changes in particle cross-section concentration.

Testing the sensitivity of the measurement to particle mass or volume concentration was somewhat less complicated. The test required that volume of particles be varied without changing the size distribution, which could be accomplished by serial dilution of an initial suspension of particles having any given distribution of particle sizes.

An initial suspension was constructed using seven different sizes of the polystyrene latex spheres to insure a smoothed $\sigma(\theta)$ curve. The initial concentration of particle volume was well above that observed on the particle-rich stations of Cruise 48. The water that was to be used to dilute the initial suspension was filtered twice through membrane filters having 0.3 μm pore diameters. A small amount of the initial suspension then was added to the diluting water to mask the optical effects of any particles still present after filtration so that the size distribution of particles in both the initial and final suspensions would be optically identical.

Scattering by the two suspensions was measured shortly after their preparation, again employing a cuvette fitted to the σ-meter to contain the samples. A series of eight sequential dilutions was then prepared by volumetric combinations of the two suspensions and submitted to the σ-meter, rinsing the cuvette between each measurement. The results of these measurements are shown in Figure 4.

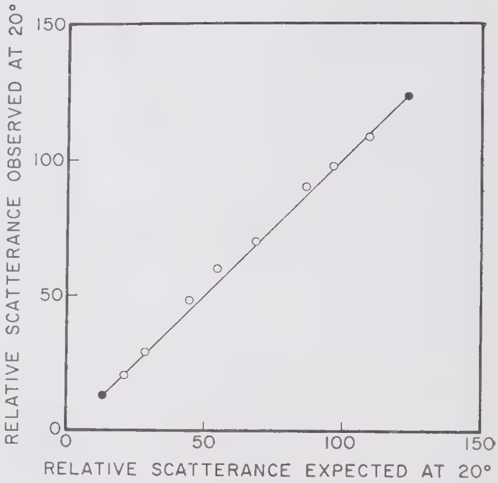

Fig. 4. Observed *vs.* expected scatterance, $k\sigma(20°)$ from serial dilutions of an initial suspension (upper solid circle) by a dilute suspension (lower solid circle).

The terminal solid circles represent the observed scattering values from the initial suspension and the diluting suspension. In the absence of multiple scattering, the expected scatterance is that which would result from measurement of any given combination of these two suspensions if the σ-meter response is linear with change in volume concentration of particles. The fit of the observed values, plotted as open circles, indicates that multiple scattering effects were negligible over the range of concentrations used, and that the σ-meter response to change in volume concentration is in fact linear.

The range of concentrations more than encompassed that observed in the ocean, in terms of $k\sigma(20°)$ values. It may therefore be stated that the σ-meter responds linearly to particle volume concentration at constant size distribution as well to cross-section concentration and is a valid tool for detection of variation of either as they occur in the sea.

4. Location and methods of field measurement

Light scattering was measured at a single forward angle using a simple, submersible instrument, the σ-meter, which consists of a projector, receiver, and depth transducer mounted on a rigid "optical bench" in a way that the receiver unit senses an optically defined, homogeneously irradiated 0.6 cm^3 segment of the collimated light beam of the projector at an angle of 20° off the forward direction of the beam. This angle was chosen to provide maximum light flux for the detector while still maintaining a well-defined forward angle. The solid angle of the projector beam is 3.58×10^{-4} sr. and that of the receiver beam is 6.83×10^{-4} sr. The light source of the projector is a tungsten-iodide cycle lamp operated at a color temperature of about 2,900 °K and is unfiltered.

A monitor cell housed in the projector provides information for regulating lamp flux. The receiver is optically filtered to yield a response peaking at 492 μm with half-band width of 37 μm. The light sensor is a multiplier phototube. Power and singnals were set between the ship and the σ-meter via multiconductor cable so that continuous measurement of scatterance was possible as the σ-meter was lowered through the upper 100 m of the sea.

Absolute calibration of the σ-meter has not yet been obtained, so that 20°-scatterance values are reported here in relative units as $k\sigma(20°)$. The constant k, relating the σ-meter signal to scatterance, $\sigma(20°)$, was evaluated at sea. Nearly simultaneous vertical profiles of scatterance at 20° were obtained at two locations in the San Pedro Channel off California using the σ-meter and a carefully calibrated scattering meter described by PETZOLD (1970). Comparison of the two sets of profiles yielded a value for k of 6.82×10^2 mv m^{-1} $sr.^{-1}$. Further details of this calibration are provided by OWEN (1972).

Particle mass, or PM, was determined by a modification of the method described by BANSE *et al.* (1963), in which the dry mass of particles retained on cellulose membrane filters is determined by the weight change accompanying filtration of known volumes of sea water. The method differs from that of BANSE *et al.* in that control filters subjected to the same environment as sample filters (except for filtration) are used as counterweights on a Cahn "Gram" Electrobalance in determining filter mass both before and after filtration, so that mass difference is measured rather than total filter mass or filter plus particle mass. This means that the filter mass is very nearly cancelled by the control filter counterweight; a low weighing scale can thus be used to assess particle mass, resulting in greater sensitivity. Also, because less water need be filtered, the filter size could be reduced. Precision at the 95% level was found to be ±6.2% of the mean, based on replicate sample determinations (OWEN, 1972).

Particle counts for measuring dispersion of particle size were made with the Coulter Counter (Model B, Coulter Electronics) using the general procedures of SHELDON and PARSONS (1967) for calibration and operation. This instrument is, in principle, capable of measuring differential particle size distributions in single water samples by repeated counts at predetermined threshold control settings. Its use in this work, however, was relegated to the secondary role, that of providing a dispersion measure that could demonstrate the uniqueness of the effective radius, for two reasons: counts in the important small size categories could not be separated from electronic noise and, second, the range of sizes that could be counted at sea was small.

Sensitivities and threshold settings of the counter were chosen to obtain particle counts in sea water samples in size categories that would give both arithmetic and logarithmic distributions according to particle cross-sectional area, the particle parameter of most direct physical influence on light scattering. Distribution of counts on the arithmetic scale was measured at 1.0 μm^2 intervals over the range from 2 to 16 μm^2 (1.6 to 4.5 μm equivalent diameters). On the geometric scale, counts were made in intervals of $2^n \mu m^2$ starting at $n=1$ through $n=10$ to measure over the range from 2 to 1,000 μm^2 (1.6 to 36 μm equivalent diameters). A 50 μm diameter orifice was used to count particles up to 6.4 μm diameter and a 100 μm orifice was used thereafter.

Water samples for PM determinations and particle counts were obtained from several depths predicated on the variation of the scattering profile, which was obtained minutes before, to characterize optically homogeneous layers and to sample the major scattering maxima and minima encountered. Water samplers were cleansed Lexan (polycarbonate) bottles. Subsequent manipulation of the water consisted of withdrawal into clean glass containers in a gentle, bubble-free flow through a 500 μm pre-filter screen.

Matching particle samples from discrete depths with corresponding values on the vertical profile of scatterance obtained up to 20 minutes previously appeared to have created error because the time intervals between observations represent at least part of the period possible for internal wave displacement under the stability conditions computed from measurements of temperature and salinity profiles. Väisälä frequency, representing the highest frequency possible for stable (non-breaking) internal waves, ranged on the examined stations from 0.0140 to 0.0356 $\sec^{-1}$ in the most stable part of the water column. The internal wave period indicated was thus short enough to have changed the geometric depths sampled between casts.

To reduce these matching errors, alternate values of scattering were computed by moving the scattering profile vertically (as would happen over an internal wave cycle) to obtain the closest agreement between extremes of the scattering and particle profiles in the density discontinuity layer. This adjustment was made only when there was a consistent mismatching of the profiles, and the resulting "best-fit" light scattering values have been used separately as alternatives.

5. Results and conclusions

The field program was conducted in part to determine the relationship of light scattering to cross-section concentration of natural particles, to define the variability of scattering, and to determine independently the size and mass of optically-active particles. Measurements were made to 100 m depth at several stations in each of four areas of the Pacific: off Baja California; off La Jolla, California; off Oahu, Hawaii; and in the mid-North Pacific along 140°W to provide a variety of oceanographic conditions. Cruise and stations are shown in Figure 5.

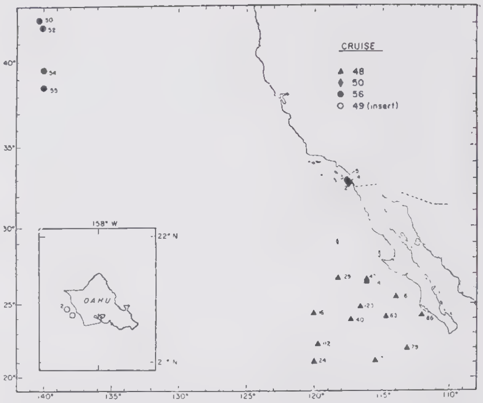

Fig. 5. Cruise and station locations of measurements of light scattering and particle characteristics.

Confirmation of laboratory results that light scattering at 20° provides a linear measure of particle cross-section concentration was sought under field conditions by comparison of scatterance from σ-meter profiles with particle cross-section concentrations as measured over a truncated size range by the Coulter Counter, as described above. Parallel work (OWEN, 1972) has shown that the frequency distribution of particle size in the open sea is approximately steady, resulting in a quasi-stationary distribution (QSD). This condition implies that size distributions determined over a limited range of sizes are directly proportional to the total, and therefore that particle cross-section evaluated over a truncated interval is proportional to total cross-section concentration.

The degree to which field measurement of $\sigma(20°)$ represents cross-section concentration of natural particles is shown Figure 6. Data pairs are from observations at Cruise 48 stations off Baja California (Figure 5). Regression analysis was performed separately on data pairs from the upper mixed layer and from the underlying pycnocline layer because small differences in the QSD of each layer might have given somewhat different scattering responses. The analysis indicates, however, that the two layers are indistinguishable by these data and that the relationship is described by the solid line of

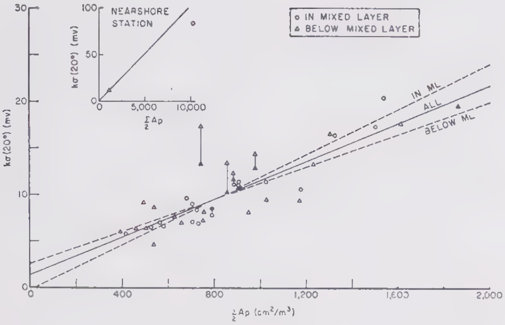

Fig. 6. Response of $k\sigma(20°)$, measured *in situ*, to concentration of particle cross-section, $\sum_{2}^{1000} A_p$, off Baja California. The computed regression equation for all points except those shown in the insert is $k\sigma(20°)=0.01016(\sum A_p)+1.42$; the correlation coefficient is 0.898. Solid symbols represent scattering values adjusted by the amount shown to reduce profile matching error described in text.

Figure 6. The computed correlation coefficient of 0.898 connotes a high degree of correlation, considering the error of measurement of cross-section concentration and the profile matching error discussed previously.

Light scattering had a characteristic vertical profile that was somewhat predictable from the physical structure of the water column. In each of the four areas, scatterance typically was nearly constant with depth over the upper mixed layer (defined by isopycnal conditions), increased to a major maximum in the upper part of the pycnocline, then decreased more gradually with depth. At the greatest depths usually measured (about 100 m), scatterance was less than that in the mixed layer.

Within the mixed layer at each location, the observed variance of scatterance was less than 5% of the mean on most stations and exceeded 10% on only three stations out of 28-one station off La Jolla, California and two stations off Oahu, all near land.

The major maximum, usually accompanied by extremums of lesser magnitude, was variable in its magnitude and its relation to other σ-profile features. It was present at 18 of the 24 stations occupied for routine data collection. Where present, the major maximums ranged in magnitude between 1.1 and 2.3 times the mixed layer scattering, averaging about 1.6. This maximum exhibited the most variation of any segment of the profile. The first or uppermost maximum was also the major maximum on 16 of the 20 stations exhibiting maximums. The depth to the major maximum was variable, apparently depending on the depth of the upper pycnocline; in no case was the maximum located in the mixed layer but always in the upper part of the pycnocline.

The deepest part of the measured layer (90 to 100 m), well within the pycnocline, exhibited considerably less scatterance variation than either mixed layer or upper pycnocline although part of the deep variation probably was due to the varying proximity of the overlying pycnocline to this fixed depth. Considering also that the euphotic layer is the principal and original source of particles in the open sea, it is to be expected that variation would decrease with depth below it, but it is surprising to see so striking a decrease of the variation so close to the source layer.

Both direct and inverse scattering problems may require knowledge of the connection between light scattering and bulk characteristics of the particle ensembles that occur in natural waters, either to use scattering to measure particle load or vice versa, or to use their ratio, specific scatterance, as a parameter of size distribution or of composite refractive index of scatterers. This knowledge is needed for an important class of problems in oceanography concerned with physical and biological effects of suspended particles.

That scatterance is directly related both in theory and by observation to cross-section concentration implies the sensitivity of scatterance to bulk concentration and to size distribution of the scatterers. Thus the degree to which scatterance expresses particle mass or volume concentration is the degree to which the size distribution is invariate from sample to sample.

Using specific scatterance, as defined by the ratio of 20° scatterance to particle mass concentration, together with independent measures of particle size dispersion, OWEN (1972) determined that ocean areas could be defined which

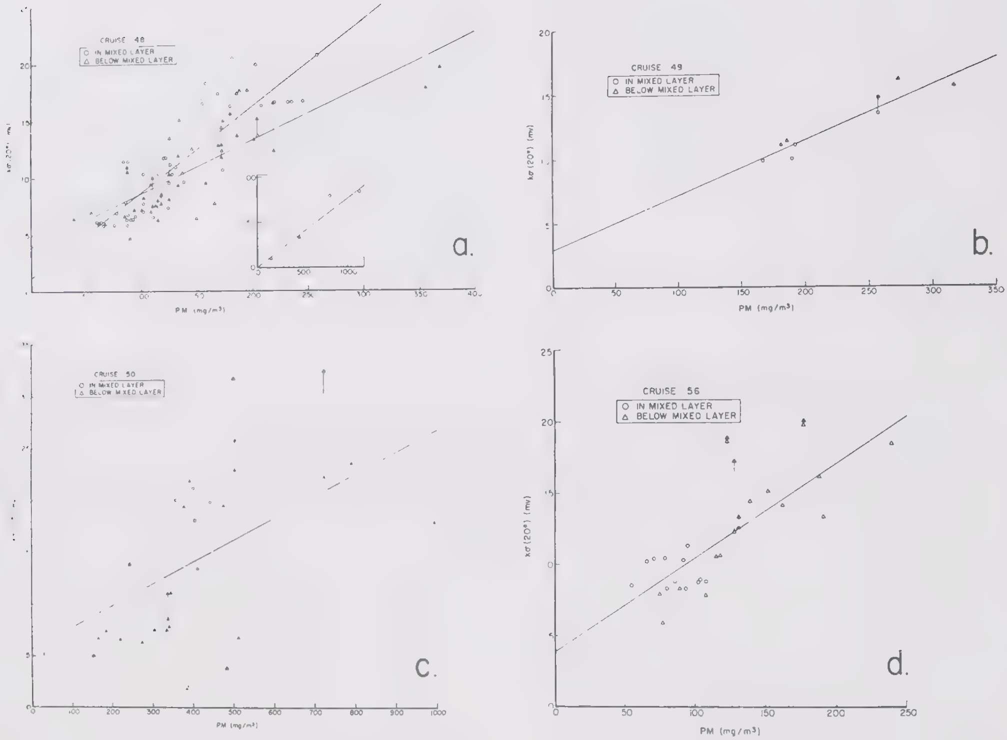

Fig. 7. Relationship of light scattering, $k\sigma(20°)$, to particle mass concentration, PM, a) off Baja California, where $k\sigma(20°)=0.075\,\mathrm{PM}+1.2$ and the correlation coefficient $r=0.87$ in the mixed layer, and where $k\sigma(20°)=0.049\,\mathrm{PM}+3.6$ and $r=0.83$ in the pycnocline; b) off Oahu, Hawaii, where $k\sigma(20°)=0.044\,\mathrm{PM}+2.6$ and $r=0.94$; c) off La Jolla, California, where $k\sigma(20°)=0.025\,\mathrm{PM}+4.8$ and $r=0.57$; d) in the mid-North Pacific where $k\sigma(20°)=0.067\,\mathrm{PM}+3.8$ and $r=0.77$.

exhibited quasi-stationary distributions of particle size and suggested a single QSD might apply over broad expanses of the open ocean. Near land, however, very different size distributions may occur, and these can be distinguished from one another by specific scatterance.

The relationship of 20° scatterance to particle mass (PM) is shown in Figure 7 for the four areas sampled. Off Baja California (Cruise 48, Figure 7a), nearshore and offshore areas were distinguished statistically by their scatterance: PM relationships but were sufficiently close to warrant their combination in this context. Further offshore, in mid-North Pacific along 140°W the scatterance: PM relationship (Cruise 56, Figure 7d) is similar to that off Baja California in terms both of the mean slope of the relationship and of the variation. This is perhaps because both locations are imbedded in the same water mass of the North Pacific gyre, although it is surprising to find that the balance of processes affecting this relationship should remain consistent between these widely separated areas.

By way of contrast, the relationship differs widely in nearshore regions, where either a different balance of processes influencing particle size results in a size distribution that alters the scatterance: PM slope, as off Oahu, Hawaii (Cruise 49, Figure 7B), or where an imbalance of processes produces a variety of size distributions as indicated by the scatter of data pairs off La Jolla, California (Cruise 50, Figure 7c).

These relationships confirm that light scattering can be used to measure bulk particle concentration (or *vice versa*) in natural waters.

It is equally apparent, however, that since scattering is sensitive to particle size distribution as well as to concentration, the use of scattering in this way is limited to domains exhibiting a common QSD. Errors of 10 % to 40 % can be incurred in the estimation of particle load by scatterance alone in oceanographically dissimilar offshore areas, and analogous comparisons between nearshore and offshore waters can err by a factor of three.

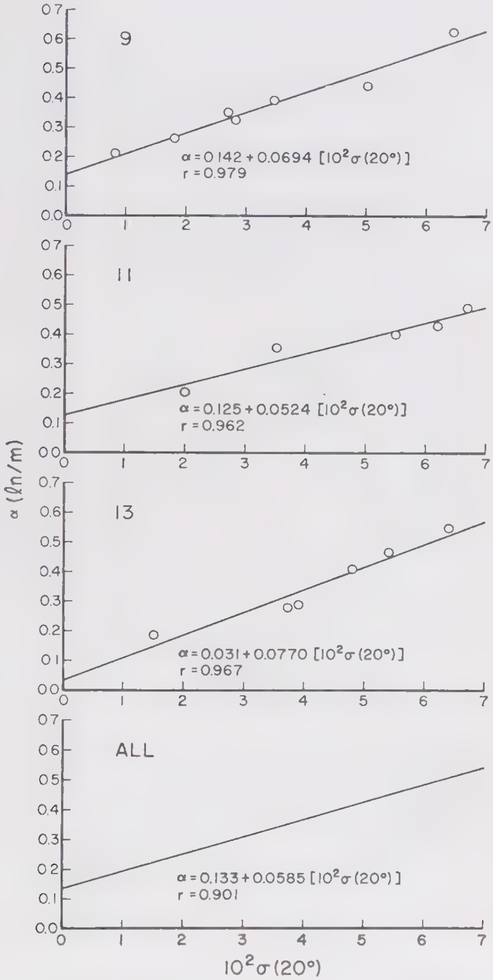

Fig. 8. Relationships of volume attenuation (α) to scatterance at one angle, σ(20°), at three stations in the San Pedro Channel. Data are courtesy of T. PETZOLD and R. AUSTIN, Visibility Laboratory, Scripps Institution of Oceanography, and were obtained with the author's help on *Jordan* Cruise 64.

Knowledge of specific scatterance is thus required for each such area before scattering alone can be said to represent particle concentration, although only a few measurements of specific scatterance need be obtained to interpret thereafter either scatterance or PM profiles in terms of the other. It follows that previous descriptions of particle content based on scattering measurements (*e.g.*, JERLOV, 1953, 1958, 1964) might be re-examined in view of this argument.

6. Estimates of relative contribution by particle concentration to natural variation of optical properties

Particulate substances variously influence the three inherent optical properties of natural sea water-characterized by the volume scattering, absorption and attenuation coefficients.

Volume scattering is almost completely controlled by particulate substances. Molecular scattering accounts for less than 6 % of the total even in clear ocean waters (JERLOV, 1968; TYLER *et al.*, 1972), and for a great deal less of the forward component of scattered light. This means that more than 94 % of scatterance is due to particles and that any change in concentration of particles of a given size distribution and refractive index will proportionately alter the magnitude of this inherent optical property.

Although light absorption by particles is usually treated as an imaginary component of the particle index of refraction, it is convenient here to consider its contribution to the volume absorption coefficient of natural sea water. The projected area of particles contained in unit volume of water from the upper mixed layer of the open ocean is typically 5 % of the projected area of the total (OWEN, 1972). If these particles absorb as little at 10 % of the light incident on them,* the absorption coefficient due to particles would be $0.005 \mathrm{m}^{-1}$, or about 13 % of observed absorption coefficients (TYLER, *et al.*, 1972) at about 500 nm, where absorption is low. This assumed value appears conservative for the present purpose of indicating the contribution of particles to absorption: *e.g.*, GORDON and BROWN (1972) find a value of $0.01 \mathrm{m}^{-1}$ appropriate in their computations in a light scattering model for Sargasso Sea waters.

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* Calculations from optical cross-sections of particles presented by BRYANT *et al.*, (1969) show that choroplasts absorb about 46 % of incident light at 480 nm, 28 % at 500 nm. The use of a 10 % value attempts to account for the unpigmented fraction of particle ensembles encounted in nature.

The third inherent optical property, the volume attenuation coefficient, is the sum of the scattering and absorption coefficients. To assess the control exerted by particles over this property it is useful to separate the effects of the water substance and its dissolved salts, which are nearly constant, from the effects of "variables" (particles and dissolved organics). At wavelengths where peak transmission occurs, the scattering coefficient accounts for about half of the volume attenuation, of which 6 % is due to water (constant) and 94 % to particles (variable) in clear ocean waters. Of the other half, due to absorption, about 50 % is due to absorption by water (constant), 13 % to particles (variable) and the remaining 37 % to dissolved organics (variable). Recombining these values results in a minimum attenuation coefficient for clear water which has a constant 27 % component due to attenuation by water, and variable components of 54 % by particles and 19 % by dissolved organics.

It is apparent from comparisons available from previous work *e.g.*, DUURSMA, 1965; MENZEL, 1970) that concentrations of dissolved organic substances are proportionately less variable than that of particulates. This qualitative statement reinforces the previous estimate that over half of the volume attenuation coefficient is controlled by particles. The observable variation of volume attenuation must therefore be even more determined by variation of particle characteristics. The partitioning of this variation between particulate and dissolved phases must be made from more definitive data, however.

The relationship of volume attenuation to scatterance at 20° is shown in Figure 8 to demonstrate the covariation of these properties. The high correlation coefficients indicate (but do not demonstrate) the control of attenuation by scattering, hence by particulate matter. The zero intercept on the ordinate may be interpreted as an estimate of the volume absorption coefficient, although there is no *a priori* reason why absorption should not co-vary with scattering.

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海中における光散乱に及ぼす粒子の影響

Robert W. OWEN, JR.

要旨: 光散乱と粒子の濃度及び大きさ分布との関係を，理論的結果を参照して，実験室内でいろいろの条件下の自然環境のもとで実験的に決めた．散乱測定と同時に粒子の個数を計測し，光散乱が粒子断面濃度の一つの尺度をあたえることを確かめた．光散乱を粒子の体積濃度の尺度としてつかうためには，粒子の大きさ分布が定常であることが必要であるが，これは海洋上層のきまった状況下では満足されている．簡単な試みによって大きさ分布の定常性を示すことが出来る．粒子が外洋水の内部性状にあたえる影響についての暫定的な推定をした．

7326

Rediscovery of Fraser's Dolphin *Lagenodelphis hosei*

F. C. Fraser[1] described *Lagenodelphis hosei* in 1956 from a skeleton collected by E. Hose[2] before 1895 on a sea beach in Sarawak. There have been no further records of the species, and its external appearance has remained unknown. We report here the nearly simultaneous, very recent rediscovery of the species in three widely separated areas of the world, and describe its external coloration and form.

On January 27, 1971, at 5° N latitude, 95° 45′ W longitude (approximately 800 km west of Cocos Island in the eastern tropical Pacific), the catch of the seiner M/V Larry Roe included approximately twenty-five dolphins of a type unknown to the fishermen. A US National Marine Fisheries Service observer aboard photographed a large male (Fig. 1*a* and *b*) and collected a small calf (Fig. 1*c* and *d*) of these dolphins. On May 20, 1972, at 5° N latitude, 122° 22′ W longitude (about 2,560 km west of the 1971 locality), three more dolphins of the same type, all females, were captured in a net set on yellowfin tuna. The specimens, heavily damaged, have been acquired by the Museum of Comparative Zoology, Harvard University.

On February 17, 1971, at 30° 47′ S latitude, 30° 58′ E longitude (approximately 80 km south of Durban, South Africa), Best, Gambell, and Ross collected a pregnant female dolphin of an unfamiliar species (Fig. 1*e* and *f*). Two days later, at 30° 09′ S latitude, 32° 20′ E longitude an adult male of the same species (Fig. 1*g*) was collected. On February 17, 1972, another specimen, an immature female (Fig. 1*h* and *i*) was taken in the same area, at 29° 33′ S latitude, 32° 12′ E longitude.

On March 1, 1971, an adult female dolphin (Fig. 1*j* and *k*) of a species unfamiliar to local residents was washed ashore at Coffs Harbour, New South Wales, Australia (30° 10′ S latitude, 153° 10′ E longitude). D. H. Brown collected the specimen and forwarded it frozen to the University of Sydney.

We have compared the prepared skeletons of the 1971 South African specimens and the eastern Pacific calf with photographs and a partial cast of the type specimen of *L. hosei* and conclude that they belong to that species. The adult specimens (Table 1) agree closely with the type in meristics, measurements, and proportions (the two skulls bracket the type in over half of the proportional measurements), and the diagnostic features of the genus and species are clearly present (Fig. 2), namely, (generic characters) "general structure of skull including tympano-periotic bones as in *Lagenorhynchus* but rostrum having a pair of deep grooves on the palatal surface and fusion of the premaxillae in the middle line dorsally . . . in the manner of *Delphinus* but not of the same extent," and (specific characters) ". . . about 8 feet [2.5 m] long, with broad cranium and basal width of rostrum about 53% of rostrum length. Rostrum flattened, premaxillae not conspicuously raised above level of adjacent maxillae and not varying much in width throughout their rostral length. Post-temporal fossae of moderate size and suboval in shape. Teeth R 44/42 L 43/ca40. Lower jaw rami with a low rounded keel in the neighbourhood of the symphysis. Teeth length 13.6–17.3 mm, their greater diameter 3.9–4.6 mm and lesser 2.4–3.7 mm. Vertebral formula—cervical, 7; thoracic 15, lumbar 21; caudal 37—total number 80 (correct within one or two)."[1]

Agreement in meristics is well within the limits of individual variation to be expected on the basis of the range of variation for other, better-known delphinids. The premaxillae of the female specimen are not fused, but incipient fusion is indicated by convergence of the bones, as in young specimens of *Delphinus*. The calf agrees well with the type in meristics, the palate is grooved and the premaxillae converge. The skeletons of the eastern Pacific specimens collected in 1972, the Australian specimen and the third South African specimen have not yet been examined, but we refer them also to *L. hosei* on the basis of their close similarity with the other South African and the earlier eastern Pacific specimens in the distinctive colour pattern and in the external size and shape.

Fraser named his new genus *Lagenodelphis* because the skull of the type possesses features of the genera *Lagenorhynchus* and *Delphinus*. *L. hosei* is in some respects intermediate in external shape (Table 2) as well. The snout is short as in

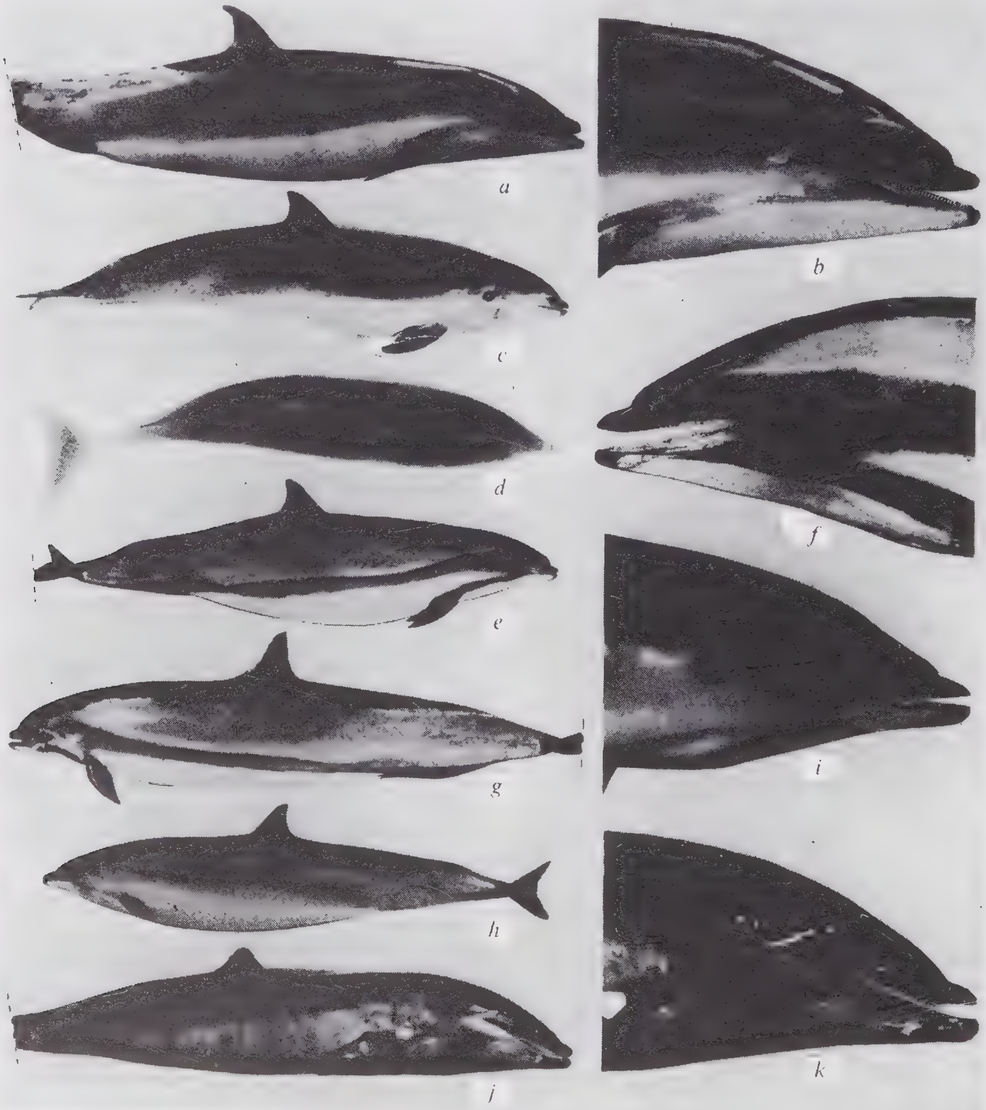

Fig. 1 *a* and *b*, Specimen LR22, male, 226 cm, from eastern Pacific. *c* and *d*, Specimen LR23, male, 110.2 cm, from eastern Pacific. *e* and *f*, Specimen PBB71/3 (SAM 36322), female, 236 cm, from off Natal, South Africa. *g*, Specimen PBB71/4 (SAM 36323), male, 264 cm, from off Natal, South Africa. *h* and *i*, Specimen PBB72/2 (PEM1517/93), female, 225.9 cm, from off Natal, South Africa. *j* and *k*, Specimen from off N.S.W., Australia, female, 226 cm.

Lagenorhynchus but well defined as in *Delphinus*. The overall build is relatively robust as in *Lagenorhynchus*, but the size and form of the appendages are as in *Delphinus*. The dorsal fin is only weakly falcate.

In a letter from Charles Hose to Sir Sidney Harmer dated October 23, 1923[1], the skin colour of the type specimen was described as "greyish or whitish yellow in parts, one might almost say cream colour, but a greyish brown in other parts. . . . The colour is difficult to describe, and it is more than twenty-five years ago." Hose's brother claimed that he had collected this specimen, and noted: "As far as I remember, it was not possible to recognize the colour of the skin, it was so very decomposed"[2]. The coloration of *Lagenodelphis* can therefore be considered as unknown. From colour transparencies of the new specimens, it can now be described as follows.

The most obvious feature is a single dark grey lateral stripe. The dorsum above the lateral stripe is dark greyish blue with a brownish hue, and the dorsal fin and both sides of the flippers and tail flukes are similarly coloured. There was a light patch in the centre of the dorsal fin of the large eastern Pacific specimen (Fig. 1*a*). The ventrum is white tinged with pink in the living and very recently killed animal. A typical delphinid bridle (terminology of Mitchell[3]) is present, with eye patch, eye stripe, blowhole stripe, and lip patch. There was a definite light grey-blue beak blaze in all animals except the calf, in which there was a suggestion of one. This blaze was bilaterally symmetrical, leaving a narrow strip of dark pigment in the midline of the beak. The blaze compresses the lip patch to a V-shaped patch at the tip of the snout and a narrow line around the edge of the gape, which connects with a similar V-shaped patch at the tip of the lower jaw.

The pattern may be considered in terms of interacting components, as has been done for other delphinids[4], as a basic "cape pattern" and a "dorsal field overlay". The ventral margin of the cape (best seen in the calf, Fig. 1*c* and *d*) arises at the apex of the melon, passes about 6 cm over the eye, dips ventrad to a low point about halfway between flipper base and dorsal fin, and then sweeps dorsad to an area between

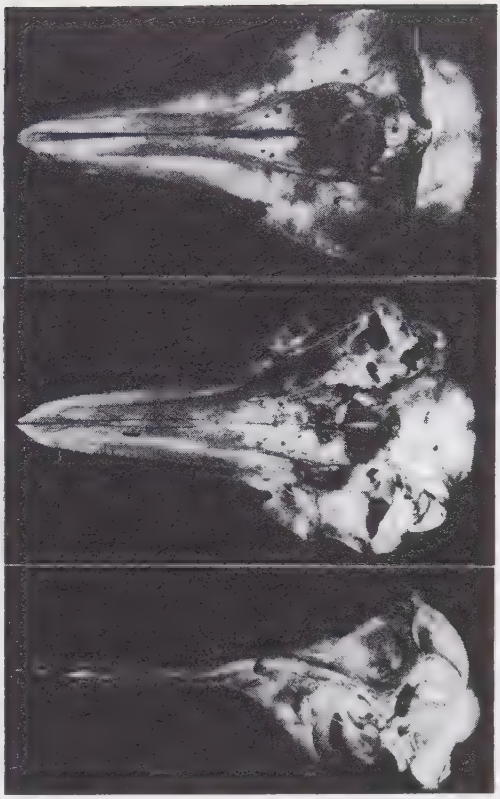

Fig. 2 Dorsal, ventral and lateral views of cranium of PBB71/4 (SAM 36323).

Table 1 Skeletal Measurements and Meristics of Four Specimens of *Lagenodelphis hosei* Fraser, 1956, including the Holotype

Measurement or count	Sarawak specimen (holotype, BMNH1895.5.9.1)* physically mature (from Fraser, 1956)	South African female PBB71/3 (SAM ‡ 36322), physically mature	South African male PBB71/4 (SAM ‡ 36323), physically mature	Eastern Pacific calf LR23 (USNM † 396079)
Condylobasal length	413 mm (100%)	429	440	
Length of rostrum	226 (54.7)	240 (55.9)	241 (54.8)	
Width of rostrum at base	121 (28.3) (53.5% of rost. ln.)	119 (27.7) (49.6% of rost. ln.)	130 (29.5) (53.9% of rost. ln.)	
Width of rostrum at midlength	71 (17.2)	71 (16.6)	80 (18.2)	
Width of rostrum 60 mm anterior to antorbital notches	85 (20.5)	86 (20.0)	101 (23.0)	
Least supraorbital width	202 (48.8)	202 (47.1)	218 (49.5)	
Preorbital width	207 (50.1)	207 (48.3)	223 (50.7)	
Postorbital width	230 (55.7)	229 (53.4)	247 (56.1)	
Zygomatic width	225 (54.5)	225 (52.4)	240 (54.5)	
Parietal width	170 (41.2)	161 (37.5)	177 (40.2)	
Maximum width of premaxillae	82 (19.9)	78 (18.2)	83 (18.9)	
Length of upper left tooth row	194 (46.9)	193 (45.0)	213 (48.4)	
Length of lower left tooth row	193 (46.7)	198 (46.2)	207 (47.0)	
Length of left ramus	350 (84.7)	367 (85.5)	375 (85.2)	
Coronoid height of left ramus	70 (16.9)	65 (15.2)	71 (16.1)	
Length of symphysis	36 (8.7)	37 (8.6)	31 (7.0)	
Number of teeth	$\dfrac{43 \mid 44}{\textit{ca.}\ 40 \mid 42}$	$\dfrac{40 \mid 42}{39 \mid 39}$	$\dfrac{42 \mid 42}{41 \mid 40}$	$\dfrac{42 \mid 42}{42 \mid 44}$
Total number of vertebrae	80 ± 2	78	78 ± 1	79
Vertebral formula	C7T15L21C37 ± 2	C7T16L21C34	C7T16L + C55 ± 1¶	C7T16L + C56§

* British Museum (Natural History), London.
† US National Museum, Washington, DC.
‡ South African Museum, Cape Town, SA.
§ Counts from radiographs of carcass.
¶ Vertical column disarticulated during preparation; 1–3 small terminal vertebrae missing.
Percentage of condylobasal length in parentheses.

dorsal fin and flukes, where it fragments into a series of diagonal lighter brushings that impart to the posterior half of the animal a chevron pattern when seen from above. The distinctive lateral stripe (eye-to-anus stripe in terminology of Mitchell[3]) is subsidiary and subparallel to the cape. It also arises at the apex and closely parallels the cape margin for about half the length of the body, diverging ventrad behind the dorsal fin and becoming diffuse above and behind the genital region.

The stripe varies markedly among the specimens in width, clearly defined length, and intensity of pigmentation, in apparent correlation with age. In the calf (Fig. 1*c*) and the subadult female (Fig. 1*h*) it is relatively narrow, passing above the eye, and becomes obscure before reaching the genital region. In the larger male from the eastern Pacific (Fig. 1*a*) (of unknown degree of maturity), the stripe is broader, encompassing the dorsal half of the eye, and is well defined for its entire length to where it interacts with the dorsal overlay system (discussed below) in the genital region. La Grange noted "considerable variation" in the intensity and definition of the stripe among the animals captured with this specimen, some having broader and darker stripes. Observations of animals at sea off the Natal Coast of South Africa indicated that pigmentation of this area was related to size of the animal. In the adult male and female from South Africa (Fig. 1*e–g*) both larger than the eastern Pacific male, the stripe is still broader, encompassing the eye completely. It appears to be broader than it actually is, however, as its ventral margin can be discerned upon close examination but is obscured by heavy pigmentation of the ventral portion of the dorsal field overlay. In the smaller specimens these two elements are distinct one from the other.

The dorsal field overlay encompasses the flipper stripe and overlaps completely the cape and eye-to-anus stripe. This feature also shows graded development correlated with size, being more lightly pigmented in the smaller specimens. There is a narrow but well-defined light line of demarcation between the anterior end of the flipper stripe and the lip patch. The flipper stripe has a double structure, which is the more clearly defined in the younger animals. The dorsal field in all the specimens has one or two thin posteriorly directed extensions that diverge from the ventral margin and run parallel for several centimetres before disappearing or rejoining the field.

In the genital region of the large eastern Pacific male (Fig. 1*a*), some interaction can be seen between the eye-to-anus stripe and the structure of the dorsal field overlay. Similar interactions between colour pattern elements may be observed in species of *Lagenorhynchus*[3]. In the South African adults the interaction is obscured by heavier pigmentation of the dorsal field in this region. Although indications strongly suggest that this and the other trends discussed above are related to development, an alternative explanation of geographical variation cannot be eliminated until known adult specimens from the eastern Pacific and other areas are compared to the South African adults.

Not seen in any of the specimens so far collected, but observed in animals at sea off the Natal coast of South Africa, is a spinal blaze (terminology of Mitchell[3]) extending from the light-coloured part of the side in a curve up towards the insertion of the dorsal fin.

Similarities in coloration of *Lagenodelphis* to any of the *Lagenorhynchus* species are difficult to demonstrate; there is no tendency towards development of a flank blaze so char-

Table 2 External Measurements of Six Specimens of *Lagenodelphis hosei* Fraser, 1956

Measurement or count	Eastern Pacific specimens		South African specimens			Australian specimen
	LR22, male, unknown degree of maturity	LR23 (USNM[*] 396079), male calf, 19.3 kg	PBB71/3 (SAM[†] 36322) adult female, 164 kg	PBB71/4 (SAM[†] 36323), adult male, 209 kg	PBB72/2 (PEM[‡] 1517/93), subadult female 130 kg[§]	———, adult female
Total length	226 cm (100%)	110.2	236	264	225.9	226
Tip of upper jaw to centre of eye	—	17.7 (16.1)	33 (14.0)	33 (12.5)	33.1 (14.7)	29.5 (13.1)
Tip of upper jaw to apex of melon	4.5 (2.0)	1.8 (1.6)	4.5 (1.9)	3 (1.1)	4.8 (2.1)	3.5 (1.5)
Length of gape	—	14.3 (13.0)	27.5 (11.7)	27 (10.2)	28.0 (12.4)	24 (10.6)
Tip of upper jaw to external auditory meatus	—	21.1 (19.1)	—	39 (14.8)	38.2 (16.9)	34.5 (15.3)
Centre of eye to angle of gape	—	4.0 (3.6)	5.5 (2.3)	6 (2.3)	6.0 (2.7)	4.4 (1.9)
Centre of eye to centre of blowhole	—	11.0 (10.0)	21 (8.9)	23 (8.7)	19.7 (8.7	17.6 (7.8)
Tip of upper jaw to blowhole	—	16.5 (15.0)	33.5 (14.2)	28 (10.6)	30.9 (13.7)	28.6 (12.7)
Tip of upper jaw to anterior insertion of flipper	—	24.5 (22.2)	46 (19.5)	43 (16.3)	45.8 (20.3)	42.0 (18.6)
Tip of upper jaw to tip of dorsal fin	—	61.0 (55.4)	133 (56.4)	132 (50.0)	118.4 (52.4)	—
Tip of upper jaw to umbilicus	—	51.5 (46.7)	110 (46.6)	116 (43.9)	106.9 (47.3)	—
Tip of upper jaw to centre of genital aperture	—	71.3 (64.7)	165 (69.9)	170 (64.4)	157.2 (69.6)	—
Tip of upper jaw to centre of anus	—	78.8 (71.5)	175 (74.2)	189 (71.6)	187.7 (83.0)	—
Projection of lower jaw beyond upper	—	0	0.3	1	0.6	0.4
Girth at axilla	—	61.7 (56.0)	110 (46.6)	—	106.9 (47.3)	—
Maximum girth	—	—	132 (55.9)	—	116.5 (51.6)	—
Girth at anus	—	37.9 (34.4)	70 (29.7)	92 (34.8)	70.0 (31.0)	—
Width of blowhole	—	2.0	2.5	4	2.5	2.4
Length of flipper, to anterior insertion	25.1[¶] (11.1)	15.2 (13.8)	27 (11.4)	28.8 (10.9)	26.7 (11.8)	25.5[‖] (11.3)
Length of flipper, to axilla	18.8[¶] (8.3)	10.5 (9.3)	19.5 (8.3)	21.5 (8.1)	20.0 (8.9)	17.3[‖] (7.7)
Width of flipper	6.6[¶] (2.9)	4.8 (4.4)	8 (3.4)	9.4 (3.6)	8.3 (3.7)	8.1 (3.6)
Height of dorsal fin	17.8[¶] (7.9)	7.6 (6.9)	17 (7.2)	22 (8.3)	15.9 (7.0)	15.0[‖] (6.6)
Span of flukes, tip to tip	49.5[¶] (21.9)	22.8 (20.7)	57 (24.1)	59 (22.3)	50.9 (22.5)	47.0[‖] (20.8)
Width of fluke, from notch to nearest point on anterior border	—	7.7 (7.0)	13 (5.5)	14.2 (5.4)	13.4 (5.9)	12.6[‖] (5.6)

Percentage of total length in parentheses. Measurements taken as specified by Committee on Marine Mammals, American Society of Mammalogists[6].

[*] US National Museum, Washington, DC.

[†] South African Museum, Cape Town, SA.

[‡] Port Elizabeth Museum, Port Elizabeth, SA.

[§] Measurements converted from inches and eighths to centimetres and tenths.

[¶] Measured 10 h after death; some dehydration probable.

[‖] Measured after exposure to Sun; some dehydration probable.

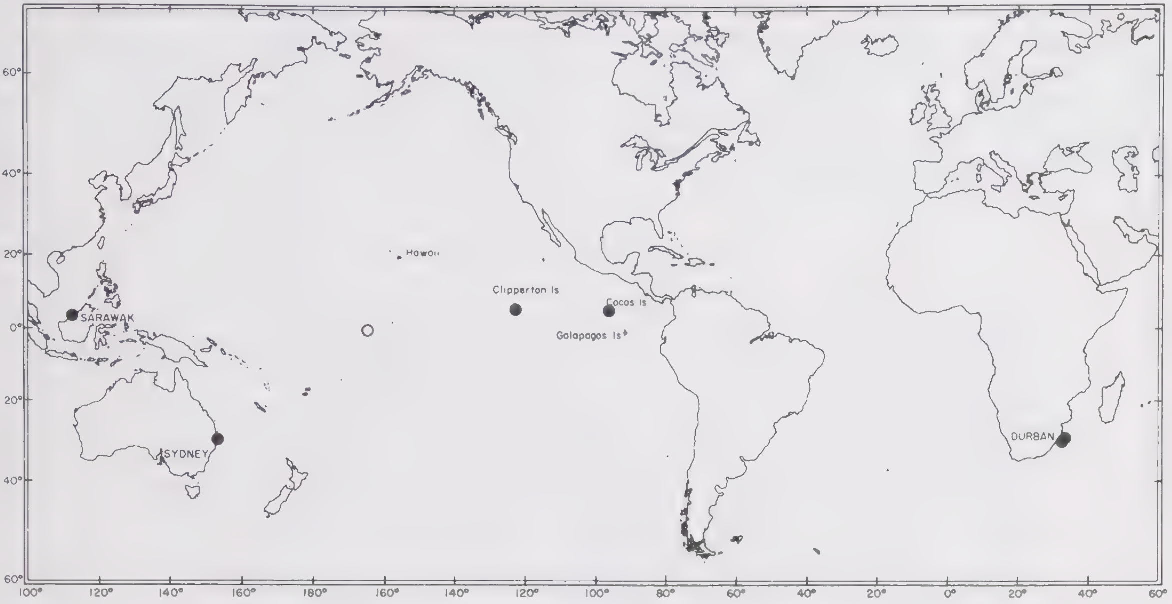

Fig. 3 Recorded occurrences of *Lagenodelphis hosei*. White circle represents sighting record.

acteristic of that genus[3], aside from the above-discussed propensity to posterior interaction of the eye-to-anus stripe and dorsal field. The species seems much closer to the *Stenella-Delphinus* group. The overall colour pattern of the adult *Lagenodelphis* is very similar to that of *Stenella coeruleoalba* with the exception of the flipper stripe, which in *S. coeruleoalba* runs to the eye or angle of gape[5], and the lack of a subtending line below the eye-to-anus stripe in *Lagenodelphis*. A comparison of the young *Lagenodelphis* with *Delphinus* reveals several features in common to both, especially if the longer beak of the latter is taken into consideration. The arrangement of the flipper stripe and eye-to-anus stripe is very similar in both species. The longer mandible of *Delphinus* seems to affect the relative position of these features, so that the flipper stripe extends farther forward in *Delphinus*, and the eye-to-anus stripe is correspondingly farther forward in the head region than in *Lagenodelphis*. *Delphinus* differs markedly, of course, in the development of a large, brightly-coloured thoracic patch (terminology of Mitchell[3]) which results from the unique partial overlap of cape and dorsal field and which is completely absent in *Lagenodelphis*.

The widely separated localities of collection reported here (Fig. 3) and the close similarity of the specimens to each other suggest that the species may be continuously distributed in high-seas tropical waters of the Pacific and Indian Oceans. It has also probably been sighted in the Central Pacific. On August 11, 1966, Balcomb observed a school of approximately four hundred dolphins at 165° W longitude on the equator (northeast of the Phoenix Islands). A field sketch and photographs (Fig. 4) clearly show the short, well-defined snout, small subfalcate dorsal fin, small flippers, chunky build, and distinct lateral dark stripe of *L. hosei*.

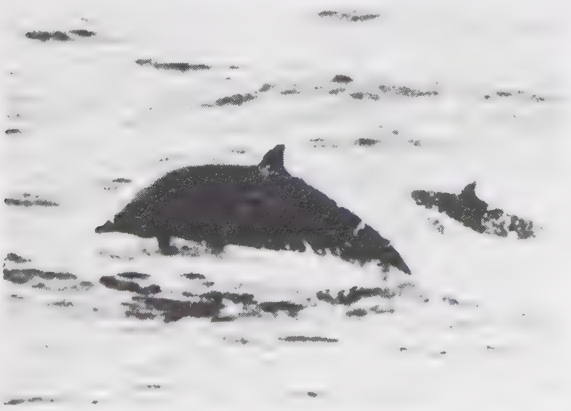

Fig. 4 Photo of dolphin sighted by Balcomb northeast of Phoenix Islands.

We thank John La Grange for collecting the eastern Pacific calf and bringing it to our attention, Captains J. Luz of the seiner Larry Roe and J. Adams of the Concho for their assistance, and James G. Mead for preparing the skull of the specimen and providing radiographs of the carcass of the calf. Captain T. Haakestadt and the crew of the whale-catcher C. G. Hovelmeier gave much valuable help in the collection of the South African specimens. We also thank David H. Brown for bringing the Coffs Harbour specimen to our attention. William E. Schevill very kindly allowed us to include the 1972 eastern Pacific record. Edward D. Mitchell provided excellent photographs of the holotype. Kenneth S. Norris, Carl L. Hubbs, and Dale W. Rice read the manuscript.

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7327

STOMACH CONTENTS OF PORPOISE, *STENELLA* SPP., AND YELLOWFIN TUNA, *THUNNUS ALBACARES*, IN MIXED-SPECIES AGGREGATIONS

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ABSTRACT

Haul-by-haul analysis of stomach contents of spotted porpoise (*Stenella attenuata*), spinner porpoise (*S. longirostris*), and yellowfin tuna (*Thunnus albacares*) from six net hauls made on mixed-species aggregations in 1968 indicates that an ommastrephid squid (probably *Dosidicus gigas*) was the most important food item in terms of co-occurrences in the three species and in terms of the volume and number. The ommastrephid occurred in significant numbers and/or volume in each haul in all the species examined, albeit to a lesser degree in the spinner porpoise than in the other two species. Overlap of elements in the stomach contents was greatest between the tuna and the spotted porpoise. In addition to the ommastrephid, the small scombrid *Auxis* sp. and epipelagic exocoetids such as *Oxyporhamphus micropterus* were important to both. The portunid crab *Euphylax dovii* was very important in the tuna but absent in both species of porpoise. Onychoteuthid and enoploteuthid squids were important in some hauls in both species of porpoise but were all but absent from the tuna. Small mesopelagic fishes, mainly myctophids and gonostomatids, were important in the spinner porpoise, but not in the spotted porpoise or the tuna. Relative frequencies of empty stomachs and state of digestion of stomach contents indicated that the spinner porpoise does not feed at the same time as the spotted porpoise and tuna. In spite of overlap among the three species in nearly all of the food components, these results suggest that the tuna and spotted porpoise feed together largely on epipelagic prey, whereas the spinner porpoise for the most part feeds deeper and at different times of day; furthermore, only the tuna eats crustaceans.

Small pelagic delphinids (*Stenella attenuata, S. longirostris,* and *Delphinus delphis*) in the eastern tropical Pacific are commonly encountered with yellowfin tuna (*Thunnus albacares*) in large mixed-species aggregations. The association between the fish and the cetaceans is very tight (Perrin, 1969, 1970). Although the reason for the association is unknown, the possibility that it is food-based immediately suggests itself. Alverson (1963) examined the stomach contents of 2,846 yellowfin tuna from the eastern tropical Pacific and found the major components to be fish (46.9% of total volume) and crustaceans (45.4%). Cephalopods accounted for only 7.6% of the volume. He encountered a wide variety of food items and changes in species composition from area to area. He therefore concluded that yellowfin tuna are nonselective feeders, foraging on whatever pelagic or benthic organisms of suitable size are locally available. Fitch and Brownell (1968) reported on fish identified from otoliths taken from spotted porpoise, *Stenella graffmani* (= *attenuata*)[4] and spinner porpoise (*S. longirostris*) caught in

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[4] The taxonomy of the spotted porpoises is confused. Recent morphological studies (Perrin, 1972) have shown that the spotted porpoise in the eastern Pacific is conspecific with the spotted porpoise that occurs around Hawaii. Accordingly, the name *S. attenuata* (Gray, 1846), which was applied by True (1906) to the Hawaiian form, is used here for the eastern Pacific form. This name has priority by date over *S. graffmani* (Lönnberg, 1934). This usage is provisional, pending the outcome of current studies comparing forms in the Atlantic and Pacific. *S. attenuata* may be a junior synonym of *S. frontalis* (Cuvier, 1829), which was described from the tropical North Atlantic.

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TABLE 1.—Collection data for stomach contents examined from yellowfin tuna, spotted porpoise, and spinner porpoise from the eastern tropical Pacific.

Net haul	Date (1968)	Location (lat., long.)	Time of day (h)	Yellowfin tuna captured (t)	Estimated composition of porpoise school: *Stenella attenuata* (No.)	Estimated composition of porpoise school: *Stenella longirostris* (No.)	Stomachs examined: *Thunnus albacares* (No.)	Stomachs examined: *S. attenuata* In field (No.)	Stomachs examined: *S. attenuata* In lab (No.)	Stomachs examined: *S. longirostris* In field (No.)	Stomachs examined: *S. longirostris* In lab (No.)
1	9 April	12°51'N, 93°18'W	1045	6	350	150			32		4
2	12 April	7°11'N, 90°32'W	1245	35	1,300	200	14		25	18	5
3	15 April	7°28'N, 91°15'W	1345	45	300		20	20			
4	16 April	7°30'N, 92°06'W	0800	60	1,500		21	24			
5	17 April	7°50'N, 92°32'W	1100	50	600		19	20			
6	18 April	7°58'N, 92°56'W	1130	35	350	50	5	19		19	
Total							79	83	57	37	9

association with tuna in the eastern tropical Pacific. On the basis of knowledge about the depth distributions of the species encountered, they concluded that the spotted porpoise had been feeding within 30 m of the surface and the spinner porpoise had been feeding to 250 m or more beneath the surface. Squid remains were present in some of the stomachs examined by Fitch and Brownell but were not included in their analysis.

In view of the nonselective feeding habits of the yellowfin tuna, analysis of comparative feeding habits of tuna and porpoise in mixed aggregations must be based on stomach contents collected from two or more of the species taken together in net hauls.

In this paper we report the results of the examination of stomach contents of 79 tuna, 140 spotted porpoise, and 46 spinner porpoise, taken in seine hauls on yellowfin tuna in 1968.

MATERIALS AND METHODS

The animals examined were captured in six net hauls by a tuna seiner (Table 1). The tuna were marked with numbered dart-type spaghetti tags and placed in the vessel's refrigerated fish holds. Stomachs were subsequently collected from the marked fish and preserved entire in 10% Formalin[5] when the catch was unloaded and prepared for processing ashore. Most of the porpoise stomachs were examined in the field and only selected items of the contents preserved in 10% Formalin for later identification (Table 1). The remainder of the stomachs were from animals frozen entire and later dissected ashore. Only the contents of the forestomach (oesophageal stomach) were examined.

The tuna taken during the cruise were nearly all about 1 m long. A random sample of 50 fish ranged from 846 to 1,164 mm fork length (average 1,079 mm).

The entire contents of stomachs opened in the laboratory were rough-sorted into fish, squid, and crustacean components. Each food item was identified to the lowest possible taxon, and the volume was then measured. Whole undigested fish were identified by comparison of external characters with published keys or with identified museum specimens and species descriptions. Usually though, digestion had precluded such a procedure, so the remains were dissected and skeletal features were compared with a large series of radiographs of determined specimens from the collections of Scripps Institution of Oceanography, Fish otoliths extracted from the frozen porpoise stomachs allowed identification of completely and nearly completely digested fish. Because the tuna stomachs were initially preserved in unbuffered Formalin, it was not possible to use otoliths from those stomachs because diagnostic otolith features dissolve rapidly in an acidic solution. Some relatively intact squids (*Dosidicus gigas*, *Symplectoteuthis oualaniensis*, *Abraliopsis affinis*, and *Onykia* sp.) were found and identified in the stomach contents. Beaks from these specimens and from squids taken on the fishing grounds by dipnetting under lights at night were used to identify isolated beaks and beaks associated with otherwise unidentifiable fragments. Published and unpublished keys to cephalopod beaks and beaks from identified squids in the reference collection of the Marine Mammal Division, Northwest Fisheries Center, were also used in the identifications. Beaks from the ommastrephid squids were relatively easy to identify and separate from those of squids of other families. Although a few of the ommastrephids in the stomachs were identifiable to species, the data for the Ommastrephidae in the tables below are subdivided into only three categories: *ommastrephid A* (probably *Dosidicus gigas*), which includes positively identified *D. gigas* and those fragments (with associated beaks) and isolated beaks most probably belonging to that species on the basis of intrafamilial differences in size and darkening of the beaks; *ommastrephid B* (probably *Symplectoteuthis* sp.), which includes positively identified *S. oualaniensis* and those fragments and beaks most probably belonging to that species or another species of *Symplectoteuthis;* and *unidentified ommastrephid*, which includes those fragments and beaks identified only as from ommastrephids. The larger of the two counts of upper and lower beaks was interpreted as the minimum number of individuals represented. The only crustacean identified, *Euphylax dovii,* was present as readily identifiable nearly complete individuals or intact chelipeds. Because many of the porpoise stomachs contained both the remains (otoliths) of very small fish (myctophids, gonostomatids) and of squid, both of which eat small fish and squid, some of the fish and squid identified were almost certainly present only secondarily. The material was analyzed on a haul-by-haul basis, and the data for each haul are presented and discussed separately. Some effect of the nonselective feeding of tuna, the patchy distribution of prey items, may still be present, however. Since the material analyzed includes some stomachs that were full of relatively undigested food and some that contained only squid beaks and/or otoliths from well-digested meals, it is likely that more than one feeding may be represented in the data for some single-net hauls.

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[5] Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The presentation and analyses of the data are patterned after those in the paper by Pinkas, Oliphant, and Iverson (1971), in which both cephalopod beaks and otoliths were used to identify stomach contents of tunas. The analyses are in terms of volume (for the stomachs examined ashore only), numbers, and percent occurrence. Each of these methods distorts the picture in some way. In the numbers and percent occurrence analyses, unimportant small but numerous organisms may be disproportionately evident. The volume analyses are distorting because the various organisms are digested at different rates and because, as mentioned above, some of the contents were freshly ingested while others were only the remnants of well-digested meals. Otoliths and squid beaks tend to be retained in the gut. An ideal method would involve extrapolating an estimate of the original volume of each prey item and calculating caloric content, but these approaches were beyond the scope of the project. The above caveats notwithstanding, the data do yield considerable information on the relative feeding habits of the three species in mixed aggregations.

The stomachs are considered in three categories: full, with traces, and empty. Full stomachs are defined as those containing fleshy re-

TABLE 2.—Stomach contents of spotted and spinner porpoise taken in a single net haul in the eastern tropical Pacific: Haul 1.

	Spotted porpoise, *Stenella attenuata*, 32 stomachs (22 full, 7 with traces, 3 empty)						Spinner porpoise *S. longirostris*, 4 stomachs (all full)					
	Volume		Number		Occurrence		Volume		Number		Occurrence	
Food item	ml	% of total	No.	% of total	No.	% (n = 29)	ml	% of total	total	% of total	No.	% (n = 4)
Total	7,619	100.0	6,101+	100.0	—	—	447	100.0	5,495	100.0	—	—
Fish	246	3.2	272+	4.5+	22	75.9	196	43.9	5,248	95.5	4	100.0
Exocoetidae	202	2.7	43	0.7	15	51.7	0	—	0	—	0	—
Oxyporhamphus micropterus	195	2.6	41	0.7	13	44.8	0	—	0	—	0	—
Exocoetus	7	<0.1	2	<0.1	2	6.9	0	—	0	—	0	—
Myctophidae	32	0.4	204	3.4	18	62.1	196 ml, not identified to species		3,868	70.4	4	100.0
Diogenichthys sp.	tr.	—	2	<0.1	2	6.9			3,374	61.4	4	100.0
Lampanyctus parvicauda	30	0.4	116	1.9	16	55.2			307	5.6	4	100.0
Lampanyctus idostigma	0	—	0	—	0	—			73	1.1	3	75.0
Benthosema panamense	0	—	0	—	0	—			24	0.4	4	100.0
Myctophum aurolaternatum	tr.	—	6	0.1	5	17.2			25	0.5	3	75.0
Hygophum sp.	0	—	0	—	0	—			5	0.1	4	100.0
Symbolophorus sp.	0	—	0	—	0	—			2	<0.1	1	25.0
Unid. myctophids	2	<0.1	80	1.3	13	44.8			58	1.1	3	75.0
Gonostomatidae:												
Vinciguerria sp.	tr.	—	1	<0.1	1	3.5			98	1.8	3	75.0
Bregmacerotidae:												
Bregmaceros sp.	tr.	—	2	<0.1	2	6.9			842	15.3	4	100.0
Melamphaidae	tr.	—	1	<0.1		3.5			424	7.7	2	50.0
Scopelogadus bispinosus	tr.	—	1	<0.1		3.5			413	7.5	2	50.0
Melamphaes sp.	0	—	0	—	0	—			11	0.2	1	25.0
Stromateidae	tr.	—	8	0.1	5	17.2			0	—	0	—
Cubiceps carinatus	tr.	—	3	<0.1	3	10.3			0	—	0	—
Cubiceps sp.	tr.	—	5	0.1	4	13.8			0	—	0	—
Bathylagidae:												
Bathylagus sp.	0	—	0	—	0	—			11	0.2	1	25.0
Scopelarchidae:												
Unid. scopelarchid	0	—	0	—	0	—			5	0.1	1	25.0
Unid. fish	12	0.2	13+	0.2+	10	34.5	0	—	0	—	0	—
Cephalopods	7,373	96.7	5,820	95.3	29	100.0	245	54.7	247	4.5	4	100.0
Onychoteuthidae:												
Onykia sp.	358	—	3,386	55.5	27	96.6	59	13.1	26	0.5	3	75.0
Ommastrephidae	157	—	1,569	25.8	29	100.0	47	10.4	68	1.2	3	75.0
Ommastrephid A (probably *Dosidicus gigas*)	127	—	1,108	18.2	29	100.0	47	10.4	45	0.8	3	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	17	—	216	3.5	27	93.1	0	—	0	—	0	—
Unid. ommastrephid	10	—	257	4.4	12	41.4	tr.	—	23	0.4	1	25.0

Enoploteuthidae:												
Abraliopsis affinis	3	–	672	11.0	29	100.0	69	15.3	151	2.7	4	100.0
Histioteuthidae:												
Unid. histioteuthid	tr.	-	1	0.1	1	3.5	0	—	0	—	0	—
Chiroteuthidae:												
Unid. chiroteuthid	tr.	—	3	0.1	1	3.5	0	—	2	0.1	1	25.0
Cranchiidae	tr.	—	3	0.1	2	6.9	0	—	0	—	0	—
Unid. cranchiid	tr.	—	3	0.1	2	6.9	0	—	0	—	0	—
Octopoteuthidae:												
Octopoteuthis sp.	tr.	—	1	<0.1	1	3.5	0	—	0	—	0	—
Unid. cephalopod fragments[1]	[1]6,855	-	—	—	29	100.0	70	15.5	—	—	1	25.0
Unid. cephalopod beaks	3	—	174	2.9	18	62.1	0	—	0	—	0	—
Crustaceans	2	—	2	0.1	2	6.9	6	1.3	—	—	1	25.0
Unid. isopod	2		2	0.1	2	6.9	0	—	0	—	0	—
Unid. gammarid amphipods	0	—	0	—	0	—	6	1.3	—	—	1	25.0

[1] Includes bulk of fragments of specimens identified from beaks.

mains; stomachs with traces are those containing only squid beaks and fish otoliths and/or skeletal fragments. The volumetric analyses are based on the full stomachs only. The number and occurrence analyses are based on the full stomachs and those with traces. In addition to the material collected from simultaneous catches of two or more of the three predator species, fish otoliths were examined from another 5 spotted porpoise and 14 spinner porpoise captured with yellowfin tuna in various locations in the eastern tropical Pacific (Appendix Tables 1 and 2).

RESULTS

Haul 1

Only the two species of porpoise were sampled in Haul 1 (Table 2). The results for the species are sharply divergent. For the spotted porpoise, cephalopods predominated in volume, numbers, and occurrence. Onychoteuthid, ommastrephid, and enoploteuthid squids were the major food items. Fish made up an insignificant proportion of the volume and consisted primarily of the epipelagic *Oxyporhamphus micropterus.* In the four spinner porpoise examined, squid and fish were present in all the stomachs, each accounting for about half the total volume. The species composition of the squid component of spinner stomachs was different from that in the spotted porpoise mainly in that one of the unidentified ommastrephids (type B, probably *Symplectoteuthis* sp.) was completely absent, whereas it was present in 27 of the 29 spotted porpoise. Fish, primarily myctophids, predominated in numbers, the ratio of fish to squid being almost precisely the reverse of that for the spotted porpoise. Five myctophid species were present in all four stomachs. By far the commonest fish was *Diogenichthys* sp. (probably *laternatus*). A bregmacerotid, *Bregmaceros* sp., was also found in all four stomachs and was the next most common fish, followed closely by the melamphaid *Scopelogadus bispinosus* and the myctophid *Lampanyctus parvicauda.*

Haul 2

All three species were examined in Haul 2 (Table 3). The results for the spotted porpoise

TABLE 3.—Stomach contents of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single net haul: Haul 2.

Food item	Yellowfin tuna, *Thunnus albacares*, 14 stomachs (12 full, 1 with trace, 1 empty)						Spotted porpoise, *Stenella attenuata*, 25 stomachs (14 full, 8 with traces, 3 empty)						Spinner porpoise, *S. longirostris*, 23 stomachs (5 full, 3 with traces, 15 empty)					
	Volume		Number		Occurrence		Volume		Number		Occurrence		Volume		Number		Occurrence	
	ml	%	No.	% (*n* = 13)	No.	% (*n* = 13)	ml	%	No.	%	No.	% (n = 22)	ml (*n* = 2 full	%	No.	%¹	No.	%¹
Total	1,591	100.0	177+	100.0	—	—	762	100.0	1,787	100.0	—	—	1	100.0	439	-		—
Fish	844	53.1	34+	19.2	12	92.3	140	18.4	154	8.6	10	45.5		1.8	420	100.095.7	2	100.0
Exocoetidae	525	33.0	26	14.7	10	76.9	25	3.3	127	7.1	7	31.8	0	—	0	—	0	—
Oxyporhamphus micropterus	425	26.7	21	11.9	10	76.9	25	3.3	90	5.0	4	18.2	0	—				
Cypselurus sp.	91	5.7	4	2.3	1	7.7	0	—	0	—	0	—	0	—				
Unid. exocoetid	9	0.6	1	0.6	1	7.7	tr.	—	36	2.0	5	22.7	0	—				
Scombridae:																		
Auxis sp.	137	8.6	1	0.6	1	7.7	110	14.4	1	0.1	1	4.6	0	—	0	—	0	—
Myctophidae	0	—	Contents preserved in Formalin; not examined for otoliths				tr.	—	17	1.0	6	27.3	tr.	—	321	73.1	2	100.0
Diogenichthys sp.							tr.	—	3	0.2	3	13.6			37	8.4	2	100.0
Lampanyctus parvicauda							tr.	—	1	0.1	1	4.6			1	0.2	1	50.0
Lampanyctus idostigma							0	—	0	—	0	—			7	1.6	2	100.0
Benthosema panamense							0	—	0	—	0	—			257	58.5	2	100.0
Myctophum aurolaternatum							0	—	0	—	0	—			2	0.5	1	50.0
Myctophum sp.							0	—	0	—	0	—			2	0.5	1	50.0
Symbolophorus sp.							tr.	—	1	0.1	1	4.6			3	0.7	2	100.0
Diaphus sp.							0	—	0	—	0	—			2	0.5	1	50.0
Unid. myctophids							tr.	—	12	0.7	4	18.2			10	2.3	2	100.0
Gonostomatidae:																		
Vinciguerria sp.							0	—	0	—	0				94	21.4	2	100.0
Bregmacerotidae:																		
Bregmaceros sp.							tr.	—	1	0.1	1	4.6			0	—	0	—
Melamphaidae:																		
Scopelogadus bispinosus							tr.	—	1	0.1	1	4.6			0	—	0	—
Stromateidae:																		
Unid. stromateoid							0	—	0	—	0	—			2	0.5	1	50.0
Paralepididae:																		
Unid. paralepidid							0	—	0	—	0	—			1	0.2	1	50.0
Unid. fish	182	11.4	7+	4.0	5	38.5	5	0.7	7	0.4	7	31.8			2	0.5	2	100.0
Cephalopods	363	22.8	131	74.0	13	100.0	622	81.6	1,633	91.4	22	100.0	54	98.2	19	4.3	6	75.0
Onychoteuthidae:																		
Onykia sp.	0	—	0	—	0	—	9	1.2	28	1.6	10	45.5	tr.	—	1	0.2	1	12.5

Ommastrephidae	105	6.6	89	50.3	11	84.6	114	15.0	1,476	82.6	22	100.0	54	—	14	3.2	6	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	103	6.5	74	41.8	10	76.9	74	9.7	1,220	68.3	22	100.0	54	—	14	3.2	6	75.0
Ommastrephid B (probably *Symplectoteuthis* sp.	2	0.1	15	8.5	8	61.5	40	5.3	262	14.7	20	90.9	0	—	0	—	0	—
Unid. ommastrephid	0	—	0	—	0	—	tr.	—	6	0.3	1	4.6	0	—	0	—	0	—
Enoploteuthidae: *Abraliopsis affinis*	0	—	0	—	0	—	1	0.1	109	6.1	16	72.7	tr.	—	1	0.2	1	12.5
Histioteuthidae: *Histioteuthis* sp.	tr.	—	1	0.6	1	7.7	0	—	0	—	0	—	0	—	0	—	0	—
Unid. octopod	0	—	0	—	0	—	tr.	—	1	0.1	1	4.6	0	—	0	—	0	—
Unid. cephalopod fragments[2]	258	16.2	—	—	5	38.5	498	65.4	—	—	11	50.0	0	—	—	—	0	—
Unid. cephalopod beaks	tr.	—	41	23.2	5	38.5	tr.	—	10	0.6	2	9.1	tr.	—	3	0.7	1	12.5
Crustaceans: Portunidae: *Euphylax dovii*	373	23.4	12	6.8	7	53.9	0	—	0	—	0	—	0	—	0	—	0	—
Unid. material	11	0.7	—	—	1	7.7	0	—	0	—	0	—	0	—	0	—	0	—

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[1] Only two stomachs were examined for otoliths; therefore the sample size for fish numbers and occurrence is two, while that for the cephalopods is eight.
[2] Includes bulk of fragments of specimens identified from beaks.

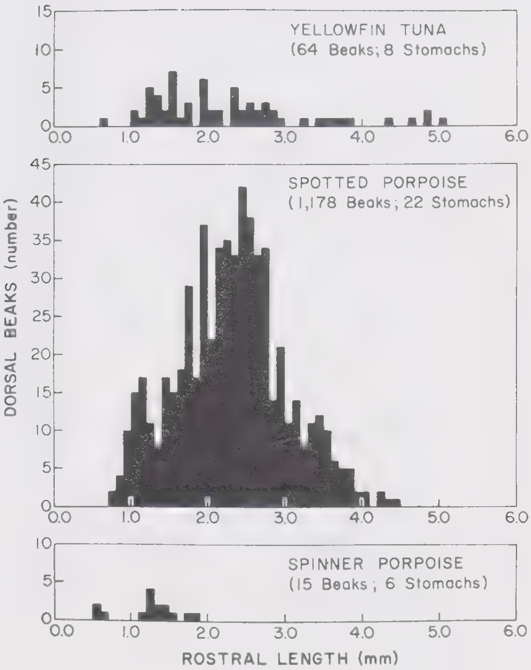

FIGURE 1.—Length frequency distributions of rostral lengths of beaks of ommastrephid squids (type A, probably *Dosidicus gigas*) from stomachs of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single-net haul (Haul 2) in the eastern tropical Pacific.

were much the same as for Haul 1, especially in that cephalopods strongly dominated in both volume and numbers. In this haul, however, ommastrephids rather than onychoteuthids predominated. Though scanty, the numerical results for the spinner were also similar to those for Haul 1. The relative squid volume was disproportionately large because the fish were represented only by otoliths. The contents of the tuna showed most overlap with those of the spotted porpoise. A scombrid, *Auxis* sp., was present in both. Cephalopods and epipelagic fish were important in both. This overlap, however, was overshadowed by some striking differences. The portunid crab *Euphylax dovii* occurred in half the tuna stomachs and accounted for a fourth of the total volume but was absent from the porpoise stomachs (both species). *Onykia* and enoploteuthid squids each occurred in about half the spotted porpoise stomachs but were absent in the tuna.

TABLE 4.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 3.

	Yellowfin tuna, *Thunnus albacares*, 20 stomachs (13 full, 3 with traces, 4 empty)						Spotted Porpoise, *Stenella attenuata*, 20 stomachs (none full, 19 with trace, 1 empty)			
	Volume		Number		Occurrence		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	No.	%	No.	%
Total	837	100.0	112	100.0	16	100.0	75	100.0	—	100.0
Fish	379	45.3	12	10.7	6	37.5	0	—	0	—
Exocoetidae	20	2.4	3	2.7	3	18.8	↓	↓	↓	↓
Exocoetus volitans	18	2.2	1	0.9	1	6.3				
Unid. exocoetid	2	0.2	2	1.8	2	12.5				
Scombridae: *Auxis* sp.	320	38.2	4	3.6	1	6.3				
Unid. fish	39	4.7	2	1.8	2	12.5				
Cephalopods	3	0.4	78	69.6	8	50.0	[1]75	100.0	19	100.0
Ommastrephidae	2	0.2	68	60.7	8	50.0	66	88.0	2	100.0
Ommastrephid A (probably *Dosidicus gigas*)	2	0.2	53	47.3	8	50.0	32	42.7	2	100.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	tr.	—	16	14.3	6	37.5	34	45.3	2	100.0
Enoploteuthidae: *Abraliopsis affinis*	0	—	0	—	0	—	9	12.0	2	100.0
Unid. Octopod	tr.	—	9	8.0	1	6.3	0	—	0	—
Unid. Cephalopod fragments	1	0.1	—	—	5	31.3	—	—	1	50.0
Unid. Cephalopod beaks	tr.	—	1	0.9	1	6.3	—	—	1	50.0
Crustaceans: Portunidae: *Euphylax dovii*	455	54.4	22	19.6	10	62.5	0	—	0	—

[1] Specimens were preserved from two stomachs only; therefore the sample size for the cephalopod taxa is two.

A striking difference between the data for tuna and spotted porpoise on one hand and the spinner porpoise on the other involved the relative number of empty stomachs encountered. Only 1 tuna stomach of 14 and 3 spotted porpoise stomachs of 25 were empty, whereas 15 spinner porpoise stomachs of 23 contained no food remains. The chance of this difference occurring by chance due to sampling error, based on chi-square analysis and assuming commonality of tuna and spotted porpoise, is less than 0.001, indicating that in the aggregation fewer spinner porpoise than spotted porpoise and tuna had been recently feeding or that the spinner porpoise had regurgitated their stomach contents during the fishing operation.

The spinner porpoise had eaten smaller squid than had the spotted porpoise and tuna. Clarke (1962) demonstrated that beak size within a species is closely correlated with total body weight. The sample of beaks of ommastrephid A (probably *Dosidicus gigas*) collected from the spinner porpoise clearly belong to a different size distribution than those taken from the spotted porpoise and the tuna (Figure 1), indicating that the spinner porpoise on the average had been feeding on smaller squid.

Haul 3

Only yellowfin tuna and spotted porpoise were examined in Haul 3 (Table 4). The porpoise stomachs were all nearly empty, containing only hard parts of squid. Except for the complete absence of fish in the porpoise stomachs, the results for the two species were similar

TABLE 5.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 4.

	Yellowfin tuna, *Thunnus albacares*, 21 stomachs (20 full, 1 empty)						Spotted porpoise, *Stenella attenuata*, 24 stomachs (23 full, 1 with traces)[1]					
	Volume		Number		Occurrence		Volume		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	ml	% (n=3)	No.	%	No.	%
Total	1,411	100.0	139	100.0	20	100.0	653	100.0	—	—	—	—
Fish	108	7.5	10	7.2	5	25.0	2	0.3	6	—	5	21.7
Exocoetidae	54	3.8	4	2.8	4	20.0	1	0.2	4	—	4	17.4
Oxyporhamphus micropterus	24	1.7	2	1.4	2	10.0	—	—	1	—	1	4.4
Exocoetus monocirrhus	0	—	0	—	0	—	1	—	2	—	2	8.7
Exocoetus sp.	29	2.0	1	0.7	1	5.0	—	—	0	—	0	—
Unid. exocoetid	8	0.6	1	0.7	1	—	—	—	1	—	1	4.4
Scombridae:												
Unid. scombrid	0	—	0	—	0	—	—	—	1	—	1	4.4
Unid. fish	54	3.7	6	4.3	2	10.0	tr.	—	2	—	2	8.7
Cephalopods	633	43.9	77	55.4	0	—	652	99.9	85	—	23	100.0
Onychoteuthidae:												
Onykia sp.	0	—	0	—	0	—	tr.	—	4	—	1	4.4
Ommastrephidae	615	42.7	38	27.3	11	55.0	650	99.5	49	—	3	100.0
Ommastrephid A (probably *Dosidicus gigas*)	609	42.3	27	19.4	10	50.0	515	78.9	35	—	3	100.0
Ommastrephid B (probably *Symplectoteuthis* sp.)	6	0.4	11	7.9	4	20.0	135	20.7	14	—	1	33.3
Enoploteuthidae:												
Abraliopsis affinis	0	—	0	—	0	—	tr.	—	31	—	3	100.0
Unid. octopod	tr.	—	1	0.7	1	5.0	0	—	0	—	0	—
Unid. cephalopod fragments	18	1.3	—	—	1	5.0	2	0.3	—	—		33.3
Unid. cephalopod beaks	tr.	—	2	1.4	2	10.0	tr.	—	1	—	1	33.3
Crustaceans:												
Portunidae:												
Euphylax dovii	700	48.6	37	26.6	14	70.0	0	—	0	—	0	—

[1] Complete contents were preserved and volumed for only three stomachs. All fish remains were preserved; therefore the sample size for fish number and occurrence is 23. For cephalopod taxa, the sample size is three.

to those in Haul 2. Overlap was greatest in the cephalopod component. The crab *Euphylax dovii* was dominant in the tuna and absent in the porpoise. The enoploteuthid squid *Abraliopsis affinis* was again present in the porpoise but absent from the tuna. Nearly all of the fish volume in the tuna was due to the presence of four frigate mackerel, *Auxis* sp., in one stomach.

Haul 4

Tuna and spotted porpoise were again sampled in Haul 4 (Table 5), and the same pattern emerged as in the previous hauls. Portunid crabs were important in the tuna but absent in the porpoise, and enoploteuthid squid were present in the porpoise but absent in the tuna. Except for *Abraliopsis*, the squid and fish components were very similar for the two species in this haul.

Haul 5

Both the tuna and the spotted porpoise in this haul were engorged with freshly ingested *Auxis* and squid (Table 6), and the makeup of the contents in both volume and number was remarkably similar. They had obviously fed on the same food at the same time. *Abraliopsis*

TABLE 6.—Stomach contents of yellowfin tuna and spotted porpoise taken in a single net haul: Haul 5.

	Yellowfin tuna, *Thunnus albacares*, 19 stomachs (all full)						Spotted porpoise, *Stenella attenuata*, 20 stomachs (17 full, 2 with traces, 1 empty)			
	Volume		Number		Occurrence		Number		Occurrence	
Food item	ml	%	No.	%	No.	%	No.	%	No.	%
Total	17,411	100.0	222	100.0	19	100.0	194	100.0	19	100.0
Fish	13,019	74.8	110	49.6	19	100.0	[1]97	<50.0	16	84.2
Exocoetidae:										
Oxyporhamphus micropterus	197	1.1	8	3.6	6	31.6	1	<0.5	1	5.3
Exocoetus volitans	107	0.6	5	2.3	4	21.1	1	<0.5	1	5.3
Unid. exocoetid	29	0.2	1	0.5	1	5.3	0	—	0	—
	61	0.4	2	0.9	2	10.5	0	—	0	—
Scombridae:										
Auxis sp.	12,720	73.1	91	41.0	19	100.0	91	<46.9	15	79.0
Unid. fish	102	0.6	11	5.0	5	26.3	5	<2.6	5	26.3
Cephalopods	4,392	25.2	112	50.5			[2]>97	>50.0	18	94.7
Onychoteuthidae:										
Onykia	0	—	0	—	0	—	present		—	—
Ommastrephidae:										
Ommastrephid A (probably *Dosidicus gigas*)	4,389	25.2	88	39.6	15	79.0	present		—	—
Ommastrephid B. (probably *Symplectoteuthis* sp.)	tr.	—	10	4.5	4	21.1	present		—	—
Enoploteuthidae:										
Abraliopsis affinis	tr.	—	3	1.4	2	10.5	present		—	—
Unid. cephalopod fragments	3	<0.1	—	—	1	5.3	—		—	—
Unid. cephalopod beaks	tr.	—	11	5.0	5	26.3	—			

[1] Fish counted in 19 stomachs.

[2] Whole squid counted in 16 stomachs not saved ; only samples of beaks were saved for identification.

was present in the tuna (beaks from three individuals), the only occurrence in tuna in the six hauls. *Onykia*, however, was again present in the porpoise but not in the tuna.

Some of the frigate mackerel were sufficiently undigested to allow them to be measured. Thirty five ranged from 18 to 29 cm fork length (average 24 cm), and sizes did not differ in porpoise and tuna.

Haul 6

Nineteen stomachs of spinner porpoise were examined in this haul, and all were empty. The spotted porpoise contained freshly ingested *Auxis* and squid (Table 7), in about the same ratio as in Haul 5, but the tuna contained only small amounts of *Euphylax dovii*, along with well-digested fish and squid remains. The three species in this haul had fed on different food and/or at different times.

Summary of Results

Ommastrephid squid A (probably *Dosidicus gigas*) was the most important prey species in terms of co-occurrence in the tuna and both species of porpoise as an important food item (Table 8). The greatest overlap between species was in Haul 5, when *Auxis* and the ommastrephid were important in the tuna and the spotted porpoise. As regards specialization, *Diogenichthys* sp., *Benthosema panamense*, *Vinciguerria* sp., and *Bregmaceros* sp. were important only in the spinner porpoise, and *Euphylax dovii* was important only in the tuna. When spinner porpoise were sampled (three hauls), the rate of occurrence of empty stomachs and the state of

TABLE 7.—Stomach contents of yellowfin tuna, spotted porpoise, and spinner porpoise taken in a single net haul: Haul 6.

	Yellowfin tuna, *Thunnus albacares*, 5 stomachs (4 full, 1 empty)						Spotted porpoise, *Stenella attenuata*, 19 stomachs (12 full, 4 with traces, 3 empty)				Spinner porpoise, *S. longirostris*, 19 stomachs (all empty)
	Volume		Number		Occurrence		Number		Occurrence		
Food item	ml	%	No.	%	No.	%	No.	%	No.	%	
Total	217	100.0	>33	100.0	4	100.0	>113	100.0	16	100.0	
Fish	68	31.3	6	18.1	3	75.0	32	<28.3	9	56.3	↓
Exocoetidae:											
Oxyporthamphus micropterus	15	6.9	1	3.0	1	25.0	0	–	0	–	↓
Scombridae:											
Auxis sp.	0	—	—	—	0	-	32	<28.3	9	56.3	↓
Unidentified fish	53	24.4	5	<15.2	3	75.0	0	—	0	–	↓
Cephalopods	tr.	—	>8	>24.2	4	100.0	[1] >81	>71.7	16	100.0	↓
Ommastrephidae	tr.	—	5	<15.2	1	25.0	↓	↓	—	—	↓
Ommastrephid A (probably *Dosdicus gigas*)							↓	↓			↓
Unidentified cephalopod beaks	tr.	—	>3	>9.1	3	75.0	↓	↓	—		↓
Crustaceans:											
Portunidae:											
Euphylax dovii	149	68.7	5	<15.2	2	50.0	> 0	—	0	—	↓

[1] Whole squid counted in 12 full stomachs, not saved; beaks not counted or saved.

digestion of the stomach contents indicated that they had not fed at the same time as the tuna and/or the spotted porpoise.

DISCUSSION

Interpretation of the feeding habits of animals from their stomach contents is complicated by two factors. First, material from the stomachs of the primary prey may be mistaken as food items of the predator. This is especially true when, as in the present study, many stomachs contain squid, which are active piscivores in their own right. However, if we are concerned only with the general depth at which feeding takes place, it makes less difference whether the fish remains found in the gut are primary or secondary in origin. When two predators show consistent differences in the probable depth origin of their stomach contents, there are at least three alternative interpretations: the two predators feed at different depth ranges (gathering the material found directly or through some secondary predator), they feed at the same depths but at different times of the day, thus taking advantage of diurnal migration of some prey species, or they feed at the same depth with one only eating prey items that were recent predators at another depth. The first explanation seems most probable.

The other complicating factor is less easy to resolve. The depth distributions of many pelagic prey items are imperfectly known. This requires that much caution be exercised when interpreting food habits of predators from data based on rare or little-known prey.

Depth Distribution of Fish

Exocoetidae

Oxyporhamphus micropterus and species of both *Exocoetus* and *Cypselurus* are all constant inhabitants of epipelagic waters. Exocoetids were extremely common in the stomachs of tuna and *S. attenuata*. Only one exocoetid otolith was found in all 46 stomachs of *S. longirostris* examined.

Scombridae

The frigate mackerel, *Auxis* sp., is another common fish of surface waters and is of relatively large size. Its occurrence in specimen stomachs parallels that of the flyingfish, often being found in *S. attenuata* and yellowfin tuna

TABLE 8.—Summary of major identified stomach constituents of yellowfin tuna, spotted porpoise, and spinner porpoise taken from mixed-species aggregations in the eastern tropical Pacific. + = present, ● = important (≥ 10% of volume and/or numbers).

	Haul number													
	1		2			3		4		5		6		
Food item	Spotted	Spinner	Tuna	Spotted	Spinner	Tuna	Spotted	Tuna	Spotted	Tuna	Spotted	Tuna	Spotted	Spinner
FISHES:														
Oxyporhamphus micropterus	+		●	+				+	+	+	+	+		(all empty)
Auxis sp.			+	●		●				●	●		●	
Diogenichthys sp.	+	●	(Otoliths not collected)	+	+	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	(Otoliths not collected)	
Benthosema panamense		+			●									
Vinciguerria sp.	+	+			●									
Bregmaceros sp.	+	●		+										
SQUIDS:														
Onykis sp.	●	●		+	+								(Squids not identified)	
Ommastrephid A (probably *Dosidicus gigus*)	●	●	●	●	●	●	●	●	●	●	●	●		
Ommastrephid B (probably *Symplectoteuthis* sp.)	+		+	+		●	●	+	●	+	+			
Abraliopsis affinis	●	●		+	+		●			+	+			
CRAB:														
Euphylax dovii			●			●		●				●		

and completely absent as a food item of *S. longirostris.*

Myctophidae

At least 13 species of myctophids were identified from specimen stomachs. A majority of the genera found (*Diaphus, Diogenichthys, Ceratoscopelus, Hygophum, Myctophum, Symbolophorus, Benthosema,* and *Gonichthys*) are known to reach the surface at night during the course of vertical migrations, but most remain deep during the day. A second group consisting of *Lepidophanes, Lampanyctus, Lobianchia,* and *Triphoturus* are usually not caught in near-surface waters, even at night; their migrations probably do not take them as shallow as the first group. Myctophids were a consistent major food item of *S. longirostris* and occasionally were common in *S. attenuata.*

Gonostomatidae

Vinciguerria is a vertical migrator found below 200 m during the day, ranging up to surface waters at night. Three-fourths of the full stomachs of *S. longirostris* examined for otoliths contained gonostomatid remains. In the much larger sample of spotted porpoise stomachs, only two contained a few gonostomatid otoliths.

Stromateidae

Although some young stromateoids are often associated with floating objects, adults have large depth ranges. *Cubiceps carinatus* has been taken in a midwater trawl station in large numbers. Stromateoids appeared irregularly in the stomachs of both species of porpoise.

Melamphaidae

Melamphaes and *Scopelagadus* adults normally remain below 100 to 200 m) Ebeling, 1962; Ebeling and Weed, 1963). Melamphaid otoliths were found occasionally in large numbers in *S. longirostris* stomachs and rarely (cf. Appendix 1) in those of *S. attenuata.*

Bregmacerotidae

Although *Bregmaceros* is known to occur bathypelagically and is captured in midwater trawls, it also can be found at the surface at night (Fitch and Brownell, 1968). It occurred regularly in low frequencies in both species of porpoises; larger numbers were found in one associated group of four porpoise (*S. longirostris*).

Gempylidae, Trachipteridae

Species of both these families have been found both in surface waters and at depth. A trachipterid otolith was found in the gut of one *S. longirostris.* Gempylid remains were found in two spinner porpoise stomachs, and in one *S. attenuata* from the far-west sampling area (Appendix 1).

Paralepididae, Bathylagidae, Scopelosauridae, Evermannellidae, Opisthoproctidae

Adult members of these families are not normally found near the surface. Most museum specimens have been caught in midwater trawls. A few otoliths from species in these families were regularly found in the stomachs of *S. longirostris.* Two specimens of *S. attenuata* caught in the far-west sampling location (Appendix 1) also contained otoliths from these families, including the only records of scopelosaurids and opisthoproctids. Otoliths from many myctophids and melamphaids were also found in these specimens. The overall pattern closely parallels that seen for spinner porpoise normally (e.g., Appendix 2). This indicates that spotted porpoise are capable of shifting to a mesopelagic feeding pattern, although epipelagic feeding appears to be typical. The cause of the shift is unknown.

Shomura and Hida (1965) reported that the stomach of a Hawaiian spotted porpoise contained fish of the families Paralepididae, Alepisauridae, Gempylidae, Bramidae, and Myctophidae, as well as squids (the major component), nemertean worms, and crab larvae. The fish component was similar to that for the two westernmost specimens of eastern Pacific *S. attenuata* discussed above.

Depth Distributions of Squids

No discrete depth sampling of squids has been carried out in the area where the animals were collected. Some information, however, is available on the depth distributions of some of the families concerned from other areas.

Ommastrephidae

The most abundant squids found in the stomachs were probably *Dosidicus gigas* and *Symplectoteuthis* sp. Clarke (1966) reported that *D. gigas* and species of *Symplectoteuthis* migrate to the surface at night. *Dosidicus gigas* and *Symplectoteuthis oualaniensis* have been taken in the area by dip net at the surface under lights at night (unpublished data). In this area, the ommastrephids are the most abundant epipelagic squids.

Enoploteuthidae

The enoploteuthid squid *Abraliopsis affinis* occurred next in abundance to the ommastrephids. It is a mesopelagic species. Gibbs and Roper (1972) stated that enoploteuthids undergo diurnal vertical migrations. It appears that this species may move into or is resident within the diving ranges of the two species of porpoise, but does not occur regularly in the possibly more epipelagic range of the tuna. Another possibility, of course, is that it is fed on selectively by the porpoise and not by the tuna.

Onychoteuthidae

Onykia sp. was not found in the stomachs of *Thunnus* and has not been taken by dip net at the surface in the area. However, it was found in the stomachs of the two species of porpoise and may be a mesopelagic species. Other members of the family, *Onychoteuthis* sp. for example, are regularly taken at or near the surface at night.

SUMMARY

While there is great overlap among the diets of the two porpoises and the tuna in mixed aggregations, there is evidence of specialization in prey items, time of day at which feeding occurs, and possibly in maximum feeding depth. Although the three species are intimately associated in tight mixed groups, they do not necessarily feed on the same items at the same time in the same place. If the association is food-based, however, the epipelagic ommastrephid squids seem to be the most probable candidates for a binding common factor in this region. The apparent trophic relationships among the three species can be crudely summarized in terms of taxa and depth distribution of the major prey items (Figure 2).

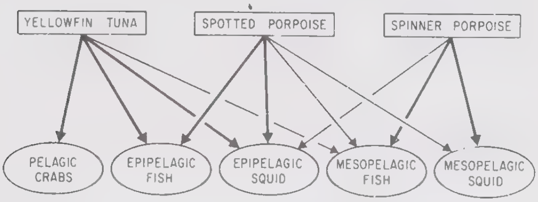

FIGURE 2.—Summary of apparent relative feeding habits of yellowfin tuna, spotted porpoise, and spinner porpoise in mixed aggregations in the eastern tropical Pacific, based on stomach-content data presented here and in Fitch and Brownell (1968) and Alverson (1963). Widths of lines crudely approximate relative importances of the major food categories.

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APPENDIX TABLE 1.—Fish identified from otoliths taken from stomachs of five spotted porpoise, *Stenella attenuata,* caught with yellowfin tuna in the eastern tropical Pacific. When more than one stomach in sample, frequency of occurrence given in parentheses. Data supplement those in Tables 2-7.

Fish	Locality			
	1	2	3	4
	7°47′N 106°50′W 18 April 1969 (1 stomach)	7°-8°N 106°-107°W 27-28 April 1969 (1 stomach)	4°-7°N 86°-100°W June-July 1970 (1 stomach)	9°28′N 129°18′W 12 Aug. 1970 (2 stomachs)
	(minimum number of individuals)			
Exocoetidae:				
Cypselurus sp.			2	
Exocoetus sp.			1	9(2)
Oxyporhamphus sp.				2(2)
Unid. exocoetid(s)	2	3		
Myctophidae:				
Diaphus spp.				34(2)
Diogenichthys laternatus				62(2)
Hygophum spp.				4(2)
Lampanyctus spp.				340(2)
Lepidophanes sp.				12(2)
Myctophum spp.				6(2)
Symbolophorus sp.				26(2)
Unid. myctophids	6		1	76(2)
Melamphaidae:				
Melamphaes spp.				18(2)
Scopelogadus sp.				29(2)
Gonostomatidae:				
Unid. gonostomatid				4(1)
Stromateidae:				
Cubiceps carinatus				9(2)
Cubiceps sp.			1	
Unid. stromateoids				5(2)
Gempylidae:				
Unid. gempylid				3(1)
Paralepididae:				
Unid. paralepidid				3(2)
Bathylagidae:				
Bathylagus sp.				23(2)
Bregmacerotidae:				
Bregmaceros sp.				2(2)
Scopelosauridae:				
Scopelosaurus sp.				1
Opisthoproctidae:				
Dolichopteryx sp.				1
Evermannellidae:				
Evermannella sp.				2(1)
Total	8	3	5	671

APPENDIX TABLE 2.—Fish identified from stomachs of 14 spinner porpoise *Stenella longirostris*, caught with yellowfin tuna in the eastern tropical Pacific. When more than one stomach in sample, frequency of occurrence given in parentheses. Data supplement those in Tables 2-7.

	Locality					
Fish	1 7°-8°N 106°-107°W 26-27 Apr. 1969 (4 stomachs)	2 7°-8°N 107°W 28 Apr. 1969 (2 stomachs)	3 3°-10°N 110°-120°W June 1970 (1 stomach)	4 10°19′N 135°38′W 5 Aug. 1970 (1 stomach)	5 9°47′N 133°25′W 11 Aug. 1970 (5 stomachs)	6 9°10°N 128°-136°W Aug. 1970 (1 stomach)
Exocoetidae:						
Oxyporhamphus micropterus	1					
Myctophidae:						
Ceratoscopelus sp.	6(1)		1			1
Diaphus spp.	102(3)	3(2)	57	1	191(5)	58
Diogenichthys laternatus			624	5	3,347(5)	398
Diogenichthys sp.	8,732(3)	109(1)				
Hygophym spp.	100(1)	3(1)	4		60(5)	7
Lampanyctus parvicauda	8(3)	2(2)				
Lampanyctus idostigma	111(2)	10(1)				
Lampanyctus spp.			613	163	2,369(5)	899
Lepidophanes sp.			14		131(4)	15
Lobianchia dofleini			239		582(5)	236
Myctophum aurolaternatum	195(2)	1				
Myctophum spp.					10(3)	
Symbolophorus sp.	17(2)		12	1	38(5)	9
Benthosema panamense	68(2)	12(2)				
Gonichthys tenuiculum	79(2)					
Triphoturus sp.	3(1)					
Unid. myctophids	115(4)	29(1)			179(4)	8
Melamphaidae:						
Melamphaes spp.	6(1)	1	2		42(2)	
Scopelogadus bispinosus	1	2(1)		49		
Gonostomatidae:						
Vinciguerria sp.	32(2)	4(1)	50		55(5)	42
Unid. gonostomatids			2		52(2)	1
Stromateidae:						
Cubiceps carinatus	10(1)	1	1	6	2(2)	4
Cubiceps sp.					2(1)	
Unid. stromateoids	3(2)		3		3(2)	2
Gempylidae:						
Unid. gempylid				2	1	
Paralepididae:						
Unid. paralepidid			2			
Bathylagidae:						
Bathylagus sp.	22(1)		11		2(1)	5
Bregmacerotidae:						
Bregmaceros sp.	1		2		9(4)	1
Evermannellidae:						
Evermannella sp.	5(1)		1		2(2)	
Stomaitidae:						
Unid. stomiatoids	1		1			
Trachipteridae:						
Trachipterus fukuzakii	1					
Total	9,619	177	1,639	227	7,167	1,686

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7328

Questions of Strategy in Fishery Management and Development[1]

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Fishery management draws on the fields of management in general, development, and fishery management. To make significant advancements in fishery management we need to invest in institutions that are capable of asking the right questions, to develop efficient means of making the proper decisions in respect to these questions, and most importantly, to develop the capability to effect actions which will facilitate these decisions.

We need to consider the complexity of the decision environment, and to have techniques for handling this complexity by insisting on analysis rather than intuition and on treating the fishery development problem as a system. The multiple-objectives problem needs to be grasped, and the questions of population dynamics need to be recast to explain departures from the existing simple models. We should consider in more detail the mathematics of programming theory. The most striking concept offered in this paper is that fishery management and development seem to be more preoccupied with tactics than with strategy.

The first concept of fishery management involves the complexity of the decision environment, resulting from increasing technological capability, the rising number of international differences, increasing communication among states, and the aspirations of developing countries.

The second is that because of these complexities more careful judgements must be made, and the scientific method employed more rigorously, including the use of systems analysis.

This requires that we view fisheries as systems, with resource problems separate from biological problems.

The fourth concept is that a broader view must be taken of the management process itself, which must be reviewed as a system. Further, management must appreciate biological, social, economic, and political objectives, and their complex interrelations. Many fisheries are said to be overcapitalized, but there have been few if any computations of optimal capital budgets, and little practical advice on strategies that can be followed by entrepreneurs. Economic objectives must be integrated into all the other objectives.

Biological questions relate to stock and recruitment, yield per recruit, and relation between catch and effort. The phenomena related to these processes are not sufficiently understood to produce predictions useful for management purposes. Some of the models used up to now are outmoded, mostly because they tell us how much can be caught from a single stock, while many stocks may be under exploitation simultaneously. Further, they do not face the major problem in fishery management — that of dividing the catch among those who wish to participate in the harvest. Divisions currently made do not always make sense from the economic or social point of view, and sometimes do not make biological sense. As an index of "sense" we might consider the benefits that could be accrued from a resource if it were owned by a single individual.

The mathematics of modelling for allocation of the catch is easy but the philosophical question of how to evaluate the various elements of the fishing process is not clear. Yet mathematical treatment allows a sharper focus of the problems, and allows us to look at a broader set of decision questions.

The sixth concept is that we need to achieve a simplification of our system. The most important simplification is to partition the problems into those that involve strategy, those that involve tactics, and those that involve operations. For development we wish to maximize the efficiency with which we transform resources into utility. There has been a general disappointment in the performance of development in recent years, and it is clear that economic criteria alone are not suitable for guiding development policy. Social welfare must also be integrated into the system.

To create a favorable environment for strategic decision-making it is necessary to have institutions that consider this problem in an explicit way; of particular relevance is the applied research institution to develop strategy.

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L'aménagement des pêches fait appel aux techniques de la gestion en général, du développement et de l'aménagement du secteur halieutique. Si l'on veut accomplir des progrès notables dans l'aménagement des pêches, il faut investir dans des institutions capables de poser les questions appropriées, mettre au point des moyens efficaces permettant de prendre les décisions nécessaires en réponse à ces questions, et par dessus tout, offrir la possibilité d'appliquer des mesures qui faciliteront ces décisions.

Nous devons envisager dans toute sa complexité le contexte dans lequel les décisions doivent être prises et disposer de techniques permettant de le faire en ayant recours plus à l'analyse qu'à l'intuition et en considérant les problèmes du développement halieutique comme un système. Le problème – qui présente des facettes multiples – doit être cerné et les questions liées à la dynamique des populations doivent être réexaminés afin d'expliquer les divergences par rapport aux modèles simples existants. Nous devons examiner de plus près l'aspect mathématique de la théorie de la programmation. La notion la plus intéressante exposée dans ce document est que l'aménagement et le développement des pêches semblent se soucier d'avantage de tactique que de stratégie.

L'aménagement des pêches est caractérisé en premier lieu par la complexité du cadre de décision—complexité due à l'accroissement des possibilités technologiques, aux différences internationales toujours plus nombreuses, à une communication accrue entre les Etats et aux aspirations des pays en voie de développement.

Il est également nécessaire, en raison d'une telle complexité, de formuler des jugements plus approfondis et d'appliquer de façon plus rigoureuse les méthodes scientifiques, notamment l'analyse des systèmes.

Pour cela, il faut que nous envisagions les pêcheries comme des systèmes, où les problèmes relatifs aux ressources sont distincts des problèmes biologiques.

La quatrième notion essentielle est qu'il faut considérer dans une perspective plus vaste le processus d'aménagement proprement dit et le concevoir comme un système. En outre, l'aménagement doit tenir compte des objectifs biologiques, sociaux, économiques et politiques et de leurs corrélations complexes. On prétend que de nombreuses pêcheries sont suréquipées, mais il n'existe pratiquement pas d'estimations sur le niveau optimal des budgets d'investissement et l'on dispose de peu de connaissances pratiques sur les stratégies que peuvent suivre les entrepreneurs. Il faut intégrer les objectifs économiques dans tous les autres objectifs. Les questions biologiques touchent les stocks et le recrutement; le rendement par recrue, et le rapport entre les prises et l'effort de pêche. Les phénomènes relatifs à ces processus ne sont pas suffisamment compris pour que l'on puisse formuler des prévisions utiles aux fins de l'aménagement. Certains des modèles utilisés jusqu'à présent sont dépassés, surtout parce qu'ils indiquent uniquement la quantité pouvant être prélevée dans un seul stock, alors que plusieurs stocks peuvent être exploités simultanément. En outre, ils ne résolvent pas le problème essentiel de l'aménagement des pêches – à savoir répartir les prises parmi les pays qui souhaitent participer à la pêcherie. Les répartitions actuelles ne sont pas toujours rationnelles du point de vue économique ou social, et parfois même du point de vue biologique. On peut considérer comme critère de rationnalité les bénéfices pouvant être retirés d'une ressource si elle était possédée par une seule personne.

L'aspect mathématique des modèles pouvant servir à la répartition des prises est aisé, mais le problème théorique posé par l'évaluation des différents éléments du processus de pêche n'est pas clair. Cependant, le traitement mathématique permet de mieux définir les problèmes et d'envisager un éventail plus vaste de questions appelant des décisions.

Le sixième principe régissant l'aménagement des pêches est qu'il faut simplifier notre système. La simplification la plus importante consiste à classer les problèmes selon qu'ils nécessitent la mise en oeuvre d'une stratégie, d'une tactique ou d'opérations. En matière de développement, nous souhaitons transformer de la façon la plus efficace possible les ressources à des fins utiles. D'une façon générale, les progrès ont été décevants au cours des dernières années et il apparaît clairement que les critères économiques ne suffisent pas pour orienter une politique du développement. Des mesures de caractère social doivent également être intégrées au système.

Pour créer un cadre favorable à la prise de décisions stratégiques, il est nécessaire de disposer d'institution capables d'envisager ce problème de façon lucide; les instituts de recherche appliquée sont particulièrement désignés pour mettre au point les stratégies nécessaires.

La regulación del sector pesquero incluye aspectos generales de reglamentación, explotación y regulación específicamente pesqueros. Para lograr progresos significativos en la regulación del sector de pesca es necesario suministrar fondos a instituciones que sean capaces de plantear los problemas adecuados, preparar medios eficientes para tomar decisiones oportunas sobre estos problemas, y sobre todo, estar en condiciones de intervenir en la forma necesaria para facilitar estas decisiones.

Hemos de tener en cuenta la complejidad del proceso de decisión y contar con técnicas para abordar esta complejidad insistiendo en el análisis más que en la intuición y tratando el problema de desarrollo del sector pesquero como un sistema. Es necesario captar el problema de la multiplicidad de objetivos, y reformular los problemas de la dinámica de las poblaciones para explicar la falta de coincidencia con los modelos sencillos actualmente existentes. Hemos de examinar con más detalle la matemática de la teoría de programación. El concepto más sorprendente que presenta este documento es que la ordenación y desarrollo pesqueros parecen ocuparse más de tácticas que de estrategia.

El aspecto más immediato de la regulación del sector de pesca es el relativo a la complejidad del proceso de decisión, debido al aumento de la capacidad technológica, el creciente número de diferencias internacionales, a la communicación que existe entre los estados y las aspiraciones de los países en desarrollo.

El segundo aspecto es que, a causa de esta complejidad, es preciso ser más cautos a la hora de emitir juicios, utilizando con más rigor el método científico, especialmente el análisis de sistemas.

Para ésto es necesario considerar las pesquerías como sistemas, en los que los problemas relativos a lo recursos se diferencian de los problemas biológicos.

En cuarto lugar, es preciso tener una perspectiva más amplia del proceso de regulación, que debe examinarse como un sistema. Además, en la regulación hay que tener en cuenta los objetivos biológicos, sociales económicos y políticos, y la compleja interrelación de los mismos.

Se dice que en muchas pesquerías hay un exceso de capitalización, pero son pocos o ninguno los cálculos que se han hecho, del presupuesto óptimo de capital y apenas existen consejos prácticos sobre estrategia a los que pueden ajustarse los empresarios. Los objetivos económicos deben integrarse en todos los demás objetivos.

Los problemas biológicos se refieren a poblaciones y reclutamiento, rendimiento por recluta, y relación entre captura y esfuerzo. Los fenómenos relativos a estos procesos no se entienden lo suficiente para preparar pronósticar que sean útiles a efectos de regulación. Algunos de los modelos usados hasta la fecha han quedado anticuados, la mayoría de ellos porque no dicen cuánto se puede capturar de una población, cuando se pueden explotar simultáneamente varias poblaciones. Además no tienen en cuenta el problema principal de la regulación del sector pesquero: la división de las capturas entre quienes desean participar en la explotación. Las distribuciones que actualmente se hacen, no siempre tienen sentido desde el punto de vista económico o social, y a veces ni siquiera desde el punto de vista biológico. Se puede considerar como criterio racional los beneficios que podrían obtenerse de un recurso si fuera propiedad de un individuo.

Los principios matemáticos en preparación de modelos para la distribución de capturas son fáciles pero el problema teórico de cómo evaluar los diversos elementos del procesco de pesca no esta claro. De todas formas, el proceso matemático permite enfocar más claramente el problema y percibir una gama más amplia de problemas relacionados con la decision.

El sexto punto es que necesitamos simplificar nuestro sistema. La simplificación más importante es dividir los problemas en tres tipos: de carácter estratégico, de carácter táctico y de carácter operativo. Con el desarrollo, lo que queremos es transformar con máxima eficiencia los recursos en algo útil. En los últimos años se ha producido una desilusión general por los resultados del desarrollo, y es evidente que los criterios económicos por sí solos no son adecuados para guiar una política de desarrollo. Es preciso integrar también en el sistema todos los aspectos de previsión social.

Para crear un medio ambiente favorable para tomar una decisión estratégica es necesario contar con instituciones que examinen este problema en forma explícita. Especialmente importante es una institución de investigaciones aplicadas para preparar una estrategia.

In Oddity Land

They're a rather peculiarly mixed up band . . .
I wish you'd remind me to bring them around
We'd all sit about on the floor and the ground
And talk about this and talk about that
Until we had a Very Nice Chat.
We might try to see if we can't agree
On whether there's too much salt in the sea . . .

In Oddity Land dogs ride on merry-go-rounds
This is a merry-go-round.

But if I keep chattering this way
I'll completely forget that I set out to say . . .[2]

that the purpose of this paper is to explore the extent to which the subject of fishery management and development resides in Oddity Land. The discussion relies to some extent on the tenets of system analysis as set forth by Churchman (1968).

The subject of fishery management and development requires definition. It draws upon the disciplines of management in general, development, and fishery management. The thesis explored is that to make significant advances in fishery management and development we need to concern ourselves with constructing and investing in institutions that are capable of asking the right questions in the area of resource management and development; developing the most efficient means for making proper decisions relevant to these questions; and, perhaps most of all, developing the capability to carry out activities which will facilitate these decisions.

When questions concerning fishery management are phrased in terms of population dynamics or economics, or are given as descriptions of the status quo, the questions are stated but frequently explicit attacks are not made on the strategy in fishery management and development. The thesis in this paper is that such an attack is needed. I have assembled a collection of concepts leading to considerations that can be useful when working out a strategy for fishery management and development.

These concepts have relatively little to do with the traditional view of fishery biology or fishery economics (these will, I am sure, be dealt with adequately by other speakers). They deal with the general problem of what kinds of things we need to think of when making resource development decisions. We need to consider, among other things, the complexity of the decision environment, the

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[2] The above excerpts are from Edward Anthony's *Oddity Land* (1957).

techniques for handling this complexity by insisting on analysis rather than intuition, and that the fishery development problem should be treated as a system. The multiple-objectives problem needs to be grasped, and even the questions of population dynamics need to be recast to explain departures from the existing simple models. The mathematics of differential equations should remain as a firm foundation for contemporary management problems, but we should consider in more detail the mathematics of allocation or programming theory. Perhaps the most striking concept offered in this paper is that fishery management and development seem to be more preoccupied with tactics than with strategy. Fishery management and development appear to have avoided the expertise of development economists, whose strategies of development would deal with the entire social–political system as well as the economic and biological features of the fisheries. The most important strides are made with practical well-focused regional-scale activities that emanate in response to local problems, rather than from the interest of the academician.

The activity of management is essentially one of organizing and relating decisions. A better job of management will arise from developing a firm conceptual basis for the decision processes or rules of management. I will try to outline some of the concepts that go beyond the traditional scope of fishery management.

Complexity of Contemporary Decision Environment

The first concept involves the complexity of the present-day decision environment. This results from increased technological capability; from an increasing number of international differences generated by the influences of the developing states; from an increasing communication among states with differing political ideologies; and from the aspirations of the developing countries. The consequences of decisions that once could be analyzed by following a few relatively simple deductions must now be interpreted in the context of complex sets of interacting alternatives, as well as in the context of various secondary effects, each of which could explode into problems of even greater consequence than those originally contemplated.

This general problem of complexity in the context of development has been summarized by Gross (1972), who indicates that the world of development is favored by:
"1) more managers and administrators already familiar with various modern management practice and thought;
2) more local experts and technicians, including trainees returning from abroad;
3) more familiarity with the contributions and limitations of transnational technical assistance; and
4) more understanding by international agencies of the importance of administrative capability." However, he also notes that there are:
"1) *more complex problems:* with most developing countries facing growing difficulties in providing sufficient employment, housing, education, health services and other necessities for a rapidly expanding population;
2) *greater environmental uncertainties:* with rapid and unpredictable changes in human aspirations, social structures, coalitions of political power, government policies, and international relations in an emerging world society;
3) *more structural intricacies:* with more and larger organizations, increased specialization and professionalism, and more labyrinthine interrelations within and among organizations;
4) *more performance complexities:* with necessarily conflicting criteria governing organizational activities over large expanses of space, time, and psychic and cultural distances;
5) *uneven technological change:* with dramatic forward leaps in some areas, particularly the military, and comparative backwardness in many others;
6) *unsettling effects of technological change:* with every technological change undermining the status and power of people accustomed to the older ways of life;
7) *the obsolescence of yesterday's innovators:* with yesterday's brilliant men focusing attention on the perfection or use of techniques increasingly irrelevant to tomorrow's problems;
8) *the spreading "Fallacy of Administration as Technical Gadgetry":* with specialized techniques of analysis or control mistakenly viewed (or fraudulently advertised) as substitutes for genuine managerial wisdom, judgement and the more profound developments in managerial approaches;
9) *increased "Brain Drain":* with more modern-style managers and technicians from developing nations moving into positions of higher psychic and monetary reward in developed nations; and
10) *larger "Managerial Gaps":* with a few organizations in developing nations developing advanced managerial capabilities, while others will still not have advanced very far beyond the culture of the ox-cart, the heritage of colonialism or the crude "scientific management" of the early twentieth century."

While the goals of fishery development may at first glance depend on whether this management is to take place in a developed or developing country this does not materially affect the ensuing discussion because, as Gross observes, the first eight of the above factors apply to both. These problems are very evident in fisheries. I have given a view of this situation elsewhere (1971) and italicize in this version a passage that seems particularly appropriate to the present state of world fisheries in the setting of this Conference: ". . . where individual fishing operations can exert tremendous intensities of fishing effort and deplete a stock in a matter of weeks or months; where the number of overexploited stocks continues to grow; where some stocks continue to become virtually extinct; and *where the community of individuals who harvest and process the stocks are, in many instances, neither held accountable nor do they demonstrate a responsibility to conserve the stocks by not overfishing, by not insisting on and supporting research of relevance to fishery problems; and by not contributing needed management data or by contributing data that either contain an inordinate amount of errors or are not timely.* These complexities require that the contemporaneous manager face the above questions and answer even more complex questions concerning how resources should be allocated in the time stream, how resources should be allocated among the states, and how criteria should be established to evaluate the resources so that appropriate allocations can be accomplished."

The Need for Systems Methodology

A second concept is that because of these complexities we need to develop approaches that will efficiently sort out the best alternatives to attain our objective of better resource decisions. In the process we will need to attain further wisdom and exercise more careful judgement in developing criteria that generate an appropriate balance between the social good and the private good. We need to evaluate distinctions between goals of economic welfare and goals of social welfare. Finally we need to make the right decisions that enable us to utilize effectively the alternatives chosen.

The traditional approach in fisheries usually involves either the "muddling through" approach (see Lindblom 1959) or the scientific method. "Muddling through" is based on intuition, and while it is frequently used, there is not much to recommend it. The scientific method, as Quade (1964) pointed out as early as 1964, is not very helpful either, because it seeks contributions to knowledge, understanding, and predictive ability, whereas what we really need is a methodology that both suggests policies and offers a list of alternatives to decision-makers, along with an interpretation of the consequences of each alternative. We need a methodology that aids in the development of policy philosophy: such a method is systems analysis (see Churchman 1968; Hare 1967; Rothschild 1971, 1972b).

Systems analysis begins by formulating objectives; next, alternative ways of reaching the objectives are decided upon; criteria are then developed to judge among the alternatives; and a plan of action is formulated based upon the best alternative. The systems methodology places considerable stress upon cycling through this procedure iteratively, because in systems analyses the objectives are a variable, and after each iteration the analyst should know more about the nature of the problem than when he becan the previous cycle, thus enabling a reiteration of the objectives. The analysis essentially stops when further iterations do not yield a reformulation of the objectives.

The Need to View Fisheries as a System

The third concept is that if we are to use systems analysis to attack fisheries problems we need to view fisheries as a system or a collection of systems. These fishery systems generally constitute a resource problem or a set of resource problems, which are distinct from biological problems in that they involve the linkages between a portion of the biota and man's use of it. These linkages involve biological questions, but they are not necessarily more important components of the linkages than the social, the political, and the economic questions. For any of our fishery resources it is very difficult to demonstrate that we have properly allocated our intellectual and financial resources to maximize the efficiency of these linkages. The fundamental problem of fishery development might very well be the mobilization and allocation of financial and intellectual resources to solve natural resources problems, which by definition involves the development of algorithms or rules for making the right decisions. The inefficient mobilization or misallocations of talent are evident in many circumstances, e.g. when a fishery is managed as a single-species fishery when in fact it catches several species. Another example is when the total disciplinary spectrum is not considered, e.g. the economic aspects but not the biological problems, or vice versa. An even more insidious misallocation of talent is paying lip service to being multidisciplinary. This Conference might do so by having a section on fishery science and methodology, one that deals with the economic aspects of management and development, and a section concerned with technology, but at the end do we merely staple these components together and call this very act of stapling a multidisciplined approach. Do we return to our offices and at some mysterious future date rise, not unlike the fabled Kraken, to attend the next great stapling? Or, on the other hand, do we examine the difficulties and constraints that prevent full utilization, formulate these as problems on a practical regional scale, then proceed systematically to achieve solutions? Being only nominally multidisciplinary will not produce results of multidisciplinary utility, and because of this the more efficient multidisciplinary approaches will in the long run be discouraged.

The Need to Take a Broad View of Management

The fourth concept is that if we are to view fisheries as a system or a collection of systems, then in addition to taking a broad view of fisheries problems we must also take a broad view of the management process itself. Management must be viewed as a system (Blumenthal 1969). This has been discussed by Drucker (1969) as the "new realities" of management, which I have quoted and paraphrased as follows (1971): "... all institutions will have to make fulfilment of basic values, beliefs, and purposes a major objective of their continuing activities rather than (having) a social responsibility that restrains or lies outside their primary functions. Further, the quality of life is, in fact, a business opportunity and can be converted into profitable business. There should be more emphasis on adapting the institutions to the needs, aspirations, and potentials of the individual than on adapting the individual to the demands of the institution." Entrepreneurial innovation was not formerly intrinsic to management, but now such "... innovation will become the very heart and core of management ... Existing institutions will have to reach out for changes as an opportunity, (and) will have to learn to resist continuity." Management should also make knowledge more productive, and here Drucker points out that in the production of knowledge there is no single best way to doing a job and "... there can be no divorce of *planning* from *doing* in knowledge work."

Drucker further points out that management should "... be considered as both a science and a humanity." In this respect "... management is ... a culture and a system of values and beliefs and serves as a channel through which society can productively utliize its values and beliefs," and final emphasis is placed on noting that "economic and social development are the result of management." Thus, for example, "... there are not underdeveloped countries. There are only *undermanaged* ones."

Multiple Objectives

The fifth concept acknowledges that if management is to be developed from a rationale that includes inter alia biological, political, social, and economic considerations, then management must appreciate biological, political, social, and economic objectives. Optimizing any one of these may produce advice that is totally unrealistic. The biological, political, social, and economic objectives are by themselves complicated and the manner in which they interrelate is even more so. Additional problems are generated when we remember that the questions of interrelations among objectives must extend among states that are at different stages of development as well as among those with differing economic ideologies. The fundamental question is whether these complications really reflect some unresolvable problems, or whether they result from inadequate attention to the interdisciplinary areas. These areas really have not been examined with the same explicit attention as have the biological or the economic areas. We therefore need to examine the problems in a systematic way. Because the systems approach is iterative, after our initial formulation of the problem we may learn that the interrelations among the disciplines are really not complicated; they may simply appear to be complicated because of the lack of genuine interdisciplinary study. We will consider in turn economic, biological, development, and research objectives. Social objectives will be touched upon in the section on development.

ECONOMIC OBJECTIVES

Economic objectives involve questions of economic efficiency, the relation between marginal cost and marginal value, and the fact that the return on any investment should be favorable when compared with alternative investments (Panel Report of the Commission on Marine Science, Engineering and Resources 1969). From these higher-level goals there have been studies partitioning various returns to investment, labor, etc. (Smith, undated). While there is a growing body of literature indicating that many fisheries are overcapitalized it is somewhat curious that, to my knowledge, optimal capital budgets have not been computed for any of these fisheries; it is then logically difficult to claim overcapitalization. While theory gives us guidance on questions of economic efficiency we have not had much explicit advice on practical strategies that can be followed by fishery entrepreneurs on a practical everyday basis. Large-scale economic efficiency cannot be attained until the components of the economic system make decisions that are consonant with the rules that appertain to the larger system. The above difficulties, as well as the roots of the multiple social welfare functions, have been discussed by Crutchfield (1972). He hoped ". . . that the late 1960s marked the end of simplistic controversies over the relative merits of maximum sustained physical yield versus maximum net economic yield as the objectives of fishery management."

Crutchfield went on to review some of the basic problems of the economic and political objectives of fishery management. He identifies several troublesome issues: a, Small groups of "winners" tend to be more influential in constructing a policy that benefits the winners to a greater extent than the long-range public interest; b, There is a zero opportunity cost for what may be an apparent inefficient employment of fishermen; c, It is difficult to appraise the benefits from a fishery that fishes multiple stocks in the same geographic area (e.g. a groundfish fishery) or fisheries that are mobile, fishing several geographical areas (e.g. the U.S. tropical tuna fishery, which fishes in the eastern tropical Atlantic), in terms of benefits accruing from a single stock; d, The range in per capita incomes among countries makes the question of allocation among them difficult. In addition, Gulland (1968) shows how the international disparity among labor and other costs can encourage increased fishing effort in a fishery that is already "overfished"; e, The emphasis placed on various objectives is not the same in different political systems; different desires for foreign exchange, for "status" in fisheries, and for maintaining options for the future (the last highlights one of the essential features of these problems, which relates to the different discount rates with which the various states perceive the various objectives).

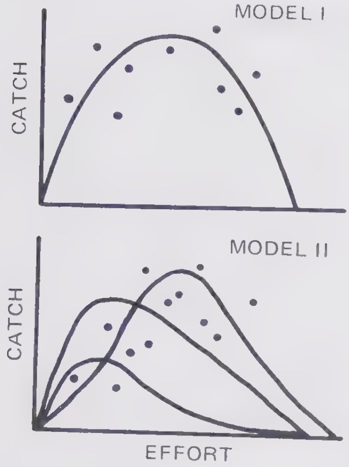
BIOLOGICAL OBJECTIVES

The biological objectives of management involve relatively simple technical computations. It is important to understand that while there are great complexities concerning the biological objectives — in particular those that concern stock and recruitment — these are relatively simple technical problems relative to the problem of taking a holistic view of fishery management and development.

The biological questions basically are related questions of stock and recruitment, yield per recruit, and the relation between catch and effort. While the question of stock and recruitment is of immense scientific importance, and an understanding of the question of the magnitude of recruitment as a function of time may very well be one of the fundamentally most important aids to fishery decision-making, the fact remains that the phenomena associated with these processes are not sufficiently understood to place general utility upon recruitment predictions for management purposes. The yield per recruit concept involves determining that combination of fishing mortality and minimum size that maximizes yield per recruit. As multiple gear fisheries become more complex, it becomes very difficult to estimate the appropriate minimum size. Besides, while it is possible to regulate minimum size by adjusting mesh, for example, it has always been difficult to adjust fishing effort. In fact, it is probably because of this difficulty that the term eumetric fishing was coined. The main value of the yield per recruit approach is to achieve an understanding of the effect of changing recruitment size, mortality rate, and growth rate upon the relation between catch and effort. This is perhaps the relation that provides the most important information for the decision-maker. I have discussed the interpretation of the relation between catch and effort in some detail (Rothschild 1971). In essence this discussion concentrates upon explaining departure from the traditional model which, using standard notation, is:

$$\frac{dP}{dt} = \phi(P) - FP$$

It is usually fitted by least squares giving a regression line so that the situation of Model I is achieved (Fig. 1). Any deviation from the line is a random component and we



strive for the equilibrium conditions represented on the line. But nature does not stand still; we cannot expect the constants in the above equations to remain constant. The "constants" are in fact random variables, and as such they are drawn from particular distributions (which we hope will remain constant). This means that each year the parameters are different and so the model then becomes as in Model II of Fig. 1.

The difference in philosophies elicited by Models I and II could be considerable. In I we always strive for the "golden equilibrium"; in II the equilibrium differs each year owing to changes in the scale of F (that is, $F = qf$ implies that q is a simple constant of proportionality between F and f, but in reality q should be considered as a functional operator ø, say, which could be complex) and changes in the stock structure and the usual vital parameters. This means that it is worth investigating the mechanisms that change the spatial distribution of the stocks, the vital parameters, and the function implied by the operator.

When integrated with economic considerations this philosophy enables a "program" (in the technical mathematical programing sense) of fishing in which by Model I we would be underfishing in some years and overfishing in others. However, our program would allocate inputs to the fishing process over a sufficiently long time such that outputs would be maximized. The methodology for such a program could be obtained from the theory of linear programing as is done in forestry or from dynamic programing, which is more realistic but sometimes computationally difficult (but note some computational simplifications in dynamic programing afforded by stochastic dynamic programing — Howard 1960). See also the analytic versions presented by Booth (1972) and Quirk and Smith (1970). Until these theories are utilized the manager will be faced with various empirical approaches such as that most recently suggested by Gulland (1972) for shrimp management:

"a) Examine the extent of the area involved, and estimate, on the basis of comparison with other areas the likely number of trawlers required for operations at the optimum level (for example 50).

b) Issue licenses for the operation of rather less than this optimum number (say 30). A condition of obtaining a license would be provision of full statistical data on the operations, including catches of each size of shrimp, fishing effort and location of fishing.

c) Allow the operation of these vessels for 2 or 3 years without modification. Then examine the statistical and other data, assess the stocks and obtain a revised estimate of the optimum number of vessels, (e.g. 55) this may be above or below the original estimate.

d) Issue further licenses to bring the total number of vessels licensed closer to, but still below, the revised estimate of the optimum (e.g. 45).

e) Make economic studies to estimate the likely profitability of each boat when the fleet approaches its optimum size.

f) Decide, particularly if this profit is large, what use should be made of it, and introduce appropriate additional conditions on license holders, e.g. substantial license fees, commitment also to land defined quantities of fish, etc.

g) Repeat steps c) to f) at intervals."

The reason that the techniques of stock and recruitment, yield per recruit, and the relation of catch-and-effort are simplistic and in a sense anachronistic is not because of any intrinsic failure in the techniques; nor is there any implication that these techniques are not extremely useful interpretative devices. The strictly biological interpretation of these models is not now a major problem since the importance of the value metric has been stressed in the literature for some decades. But it is still not generally recognized that some concepts of management can provide incentives for gross overcapacity, or that MSY as a concept can be economically disadvantageous because if it is not responsive to supply and demand it can generate undesirable fluctuations in price. The major anachronism is that these models simply advise us on how much can be caught from a single stock; but by modifying some of the growth and mortality rates they can show us how to modify the total catch. This in itself is an important problem because it involves the methodology for increasing the supply of fish, which unfortunately tends to be submerged when discussing management. The major difficulty with these models from a decision point of view is that they do not face what is perhaps the major problem in fishery management, that of dividing the catch among those who wish to participate in the harvest. The central question of fishery decision-making – fishery management – is how to allocate the resource in space and time. The other major problem is to increase the supply of fish.

We are continually answering the question of "who gets what," since as long as the catch is shared by at least two entities an allocation is performed. But allocations made implicitly do not always make sense from an economic or social point of view, and one could point to a number of examples where they do not make biological sense. As an index of "sense" we could consider the benefits that could be accrued (and then distributed) from a resource if it were owned by a single individual, and compare these to the benefits that actually accrue under post hoc ergo propter hoc allocation. The after-the-fact allocations are similar to after-the-fact policies. I have discussed the analysis remedy for after-the-fact overdetermined policies (Rothschild 1972), and the same remedy of analysis would apply to allocations.

Allocation Models

Because allocation models are so unusual in fisheries – a seeming paradox – the subject is worth a bit of discussion. For example, with respect to allocating the catch there is a rich framework in the theory of mathematical programing that deals with this. While there have been a few attempts (e.g. Rothschild and Balsiger 1971; Booth 1972; Quirk and Smith 1970), the problem has not really been addressed in depth mainly because, while the mathematics are easy, the philosophical question of how one evaluates the various elements of the fishing process is not entirely clear, although the formulation of these problems in mathematical terms can be helpful in sharpening the questions that can be asked. For example, in salmon management the traditional technique involves allowing sufficient "escapement" (the fish that escape the fishery and are therefore able to spawn). But when formulating the salmon problem as a programing problem we can give many more options to the systems design. For example, Rothschild and Balsiger (1971) maximized:

$$Z = \sum_{i=1}^{M} \sum_{j=1}^{N} c_{ij} X_{ij}$$

subject to:

$$X_{ij} \leqslant R_{ij}$$

$$\sum_{i=1}^{M} X_{ij} \leqslant K_j$$

$$\Sigma \, \Sigma \, a_i X_{ij} \leqslant T - E$$

$$\Sigma \, X_{ij} \leqslant M - \frac{E \times H}{F}$$

$$\sum_{j} X_{ij} \leqslant S_i - L_i$$

where: M = total number of age-sex categories; N = total number of days in the run; X_{ij} = number of fish caught in the ith age-sex category on the jth day of the run; c_{ij} = value of a fish caught in the ith age-sex category on day j of the run; R_{ij} = number of fish of the ith age-sex category that run past the fishery on the jth day; K_j = capacity of the cannery or canneries in numbers of fish on the jth day; a_i = average number of eggs in each fish in the ith age-sex category; T = total number of eggs contained in the escapement and catch; E = minimum number of eggs required in the escapement; M = total number of males in the escapement and catch; H = sex ratio desired in the escapement, expressed as the number of females per male; F = average fecundity of the female age-sex categories, expressed in number of eggs; S_i = number of fish in the total season run of the ith age-sex category; L_i = number of fish of the ith age-sex category desired in the season's escapement.

Putting the problem in this context allowed us to look at a much broader set of decision questions than is conventionally examined in salmon management. In the "who gets what" context we are allocating different kinds of salmon (identified by age, sex, and day of "entrance" into the fishery) among the catch, taking into account a daily processing capacity, a seasonal processing capacity, and a requirement to allow a certain number of eggs and male fish to survive the fishery for reproductive purposes. Because of the way the model was formulated we could simultaneously study the unused catch or escapement, the unused cannery capacity, and the number of eggs that could be caught and were not. The formulation further enabled us to impose a value to different sizes and sexes of fish, to a salmon egg, and to an empty unit of cannery capacity. These important values are the kinds of information that need to be accounted for in the decision process. The analysis led to further interesting results showing how fish that were ordinarily of less value could become more valuable than fish of greater value.

We have used another example of linear programing to study production functions in fisheries, where we allocated two species of tunas among three size-classes of boats to provide guidance on optimum tuna fleet composition (Rothschild 1972a). In the discussion we indicated the simple extension for allocating the catch among countries. As we try to bridge the gap between the inputs to the fishing process we can see that the usual fishing power calculations are not sufficient to measure and analyze the inputs because these have chance components that need to be handled explicitly. We developed a model for this, evaluating the quality of different decisions in terms of the entropy perceived by the decision-maker. We further gave an example of how the large variances sometimes encountered in fishery work could be treated explicitly.

In reviewing the subject of traditional dynamics we would be remiss if we did not mention the most recent advances, developed by Ricker (1948) and exemplified more or less simultaneously by Gulland (1965) and Murphy (1965), which have been facilitated by computer computation. These derive from the virtual population methods and enable the estimation of fishing effort as a function of age. The second important technique is that of generalizing the production function developed by Pella and Tomlinson (1969). For a recent discussion of the production model, see Fox (in press). For a review and detailed example of the application of these methods the reader is referred to the paper by Abramson and Tomlinson (1972).

Goals in Development

A further set of goals needs to be considered — those for development. An example of these may be found in the Provisional Indicative World Plan for Agricultural Development (FAO 1970). While these relate mostly to agriculture there is no reason why fishery development cannot be guided by them:

"a) Providing the future food supply, with population typically growing at 2.5 to 3% a year.

b) Adjusting to the still more rapid increase in the number of people who can only be reached through marketed output, as well as the changes in the compostion of the diet that accompany urbanization and rising incomes per capita.

c) Adjusting to the specific requirements in food policy, which emerge from the analysis of the main dietary deficiencies (especially protein quality) inherent in the present composition of food intake under the major dietary patterns.

d) Assuring the raw material base for the processing industries (food and non-food), which are usually dominant in the early stages of industrialization.

e) Earning and saving foreign exchange. Shortage of the latter is one of the most serious bottlenecks to economic growth in most developing countries and most of them depend mainly on agricultural products to earn it. On the other hand, in a great many countries the agricultural sector offers considerable scope for economic import substitution. In more general terms the agricultural sector has a significant part to play in the mutual enrichment of all countries through expansion of international trade based as far as possible on comparative advantage.

f) Providing a large part of the additional employment that will be needed over the period up to 1985; and at the same time permitting some of the increase in the labor force to become available for nonagricultural occupations through an increase in labor productivity on farms.

g) Contributing to the savings needed to finance development.

h) Helping in the diffusion of wealth, which alone can provide a mass market for industry, not to speak of an adequate effective market for agricultural products. The greater part of the population in most developing regions is still agricultural, so that without prosperity here, the whole process of economic development is thwarted.

i) Providing a market for "producer goods" industries, that is farm machinery and equipment, fertilizers, chemicals for control of pests and diseases."

The goals of a research organization and the kinds of information that are applicable have been discussed by Rothschild and Uchida (1968: 46–48).

Simplification Through a Distinction Between Tactics and Strategy

The sixth concept is that we need to achieve a simplification of our system, given the complexity of the contemporaneous decision environment, the availability of a methodology to handle the complexity, the need to view the fisheries as a broadly based system, the need to consider the management of a system from a similarly broad viewpoint, and the complex multiple objectives associated with fisheries. System simplification can be attained in a variety of ways (Hare 1967). One approach is to partition the problem into its components and concentrate on the most important one. Another is to rely on various mathematical techniques to help synthesize the quantitative aspects of the problem. Perhaps the most important simplification was formulated by Anthony (1965), who noted that decision problems could be divided into those that involve strategy, those that involve tactics, and those that involve operations.

In an earlier paper (Rothschild 1971) I considered Anthony's strategic tactical breakdown in terms of the fishing question in the strict sense, where the annual catch is the strategy, and the methodology of obtaining the catch is the tactics. In the present paper I follow Gross (1972), and regard the following distinctions between strategic and tactical decision-making:

Strategic approach	Tactical approach
Broad scope	Narrow scope
Long time-horizon	Short time-horizon
Formulates problem	Seeks objective answer to problem formulated by others
Systems oriented	Operations research oriented
Considers relation of problems to other problems	Considers only solution of particular problem
Concentrates on desirability	Concentrates on feasibility and consistency

If, for example, we consider tactics without considering strategy we could very well be answering the wrong questions, even though perhaps with considerable skill. For the broad questions of fishery management and development we may be concentrating on tactics without having a well developed strategy. Clearly we need to inquire as to the appropriate strategy for fishery management and development.

Development

The seventh concept is that of development. It is complicated by the fact that in the context of fisheries it can mean development in the usual sense, that is, related to the developing countries, or it can mean the development of an underdeveloped industry in a developed country. We can have a developed fishing industry in an underdeveloped country, an underdeveloped fishing industry in a developed country, or an industry undeveloped in the sense that it does not make the most efficient use of available resources.

In the international context the development of fisheries must be responsive to the general international development problem. This is reflected in a number of indices that demonstrate the gap between the "haves" and the "have nots." One commonly used index of the quality of life is the per capita GNP; poor countries are those with a per capita GNP which is less than the world mean per capita GNP (Bhagwati 1966).

There are other measures of the quality of life such as literacy, infant mortality, physicians per capita, etc. The responsibility of the developed nations for facilitating the development of the developing nations is outlined by Myrdahl (1972). Recognition of the need for international development stimulated the United Nations to consider the 1960s as the Decade of Development. While there were some increases there has been a general disappointment in the average development performance during that decade. A diagnosis of the reasons may help us to put in perspective some of the problems in the narrower field of fishery management and development. In a diagnosis of the problem associated with development during the 1960s, Robinson (1971) pointed out that the theme for generating development at that time was the "economic plan." "Essentially, the rationale of the plan was to mobilize economic resources and deploy them on cost–benefit criteria to projects with optimal effects on economic growth rates and structures." Robinson synthesized several views on the best alternative plan for development:

"The view of Ramaswami and Ikram states that in South Asia agriculture would not be a primary sector in development because farm surpluses increase at a lesser rate than rural population; only industrialization can provide a quantum jump for the economy. This industrialization would create a better capital–output ratio than would agricultural development through

- large amounts of capital quickly
- provide resources for its own development
- import substitution which saves foreign exchange."

Robinson furthermore points out that there were reservations associated with the above view of "industrialization": rapid industrialization would likely call for more foreign exchange than would be available; industries would be inefficient owing to stagnation of agricultural incomes.

If the development process concentrates upon industrial technology, then the gap between rural and urban incomes will increase, and migration into urban areas will be encouraged, but as technology advances jobs will be destroyed. This will achieve a high output–capital ratio, but the costs in terms of widespread unemployment and political unrest will be great.

Robinson (1971, p. 3) continues by quoting E. F. Schumacher:

"Industrial concentrations based on the latest technology may give you the best output for capital invested and the best rate of economic growth; but the political and human costs in unemployment in the countryside, in resentment against a policy that leaves 80% of the nation in rural areas worse off than they were before, are so great that society (may) disintegrate and the economy run down."

Dr. Schumacher suggests that the answer lies in the development of "intermediate technologies" that are prosecuted in rural as well as urban areas.

A third point of view, that of Prof. N. Kaldor, is to develop optimal capital output projects in urban areas and then redistribute the income to rural areas; but this would generate difficult political problems. It turned out that the "best of plans based on maximum productive efficiency may yet make bad economic policy." Robinson notes that . . . "the imperious, economic approach in which economic stages and models, economic factors and economic criteria reigned almost unchallenged in principle, as arbiters of development strategy. The tendency of the style was too optimistic. It exaggerated the actual power of economic over noneconomic factors . . ."

From these excerpts we can see that questions of development are wide reaching and that economic criteria by themselves are not suitable for guiding development policy. It is necessary to reconcile questions of social welfare with questions of economic growth. What all this shows is that development is not an economic process or a technological process; it is a process whereby the quality of life will be better tomorrow than it is today.

Since our goals involve increasing the supply of fish through management, increasing the supply of fish through discovery of new stocks, and developing more efficient processing and marketing linkages, we might simply develop programs to undertake attaining these three objectives. Unfortunately there are many such programs, and while they are capable of solving technical or tactical problems, there are not as many successes as one might hope in making better resource decisions. The major problem in both developed and developing countries lies in decision-making institutions, and the major problem in institutional development is that of developing an institutional strategy. This is not a fishery problem per se, but it is relevant since it is the general development problem. Gross (1971) characterizes it as being reflected in organizations that exhibit: a deep-rooted resistance to change, ritualistic rather than genuine planning, and lack of managerial (or administrative) capability. He further observes that the "world of development administration is peopled too much by dinosaurs and ostriches. The ostriches keep their heads and eyes snugly buried in the warm sands of ancient memos and bureaucratic fantasy. The dinosaurs bask in the memory of past struggles for freedom, blind to the world-shaking changes that threaten new forms of servitude. Both are encouraged in these attitudes by the example, advice, or misleading information provided by richer ostriches and more powerful dinosaurs in the so-called "developed" nations. Neither has one of the most important virtues of an administrator . . . the ability to understand rapid and complex environmental changes and help his organization adapt creatively to these changes."[3]

While in some cases the above may be an overstatement it is still quite clear that administrative ability is a considerable constraint on development.

It is generally realized that fishing problems are characterized by underlying roots of conflict generated by "who gets what," but it is not clear that the science of conflict study has been explicitly applied in the fishery area.

Institution Development

The eighth concept is that in order to create a favorable environment for strategic decision-making and the framing of problems in a strategic context, it is necessary to have institutions that consider this problem in an explicit way. While there are many institutions that relate to fisheries, there is one type particularly relevant to our considerations, the applied research institution that can provide the driving force to develop strategy. To build such an institution it is necessary to develop various properties in functional terms. We thus eliminate the usual organizational hierarchy and provide the research institution with a strategy instead of merely factors of the organization. A functional organization might include the following: clearly identified strategies and tactical components; clearly identified participants, operations, and functions; an acknowledgment that participants include "customers" and that an organization's goals can be determined by conducting market research upon the customers; a specific mechanism for communicating with customers; a group of individuals with the specific task of providing accountability in the system; flexibility in program structure so that the tactical operations consist of a mix of

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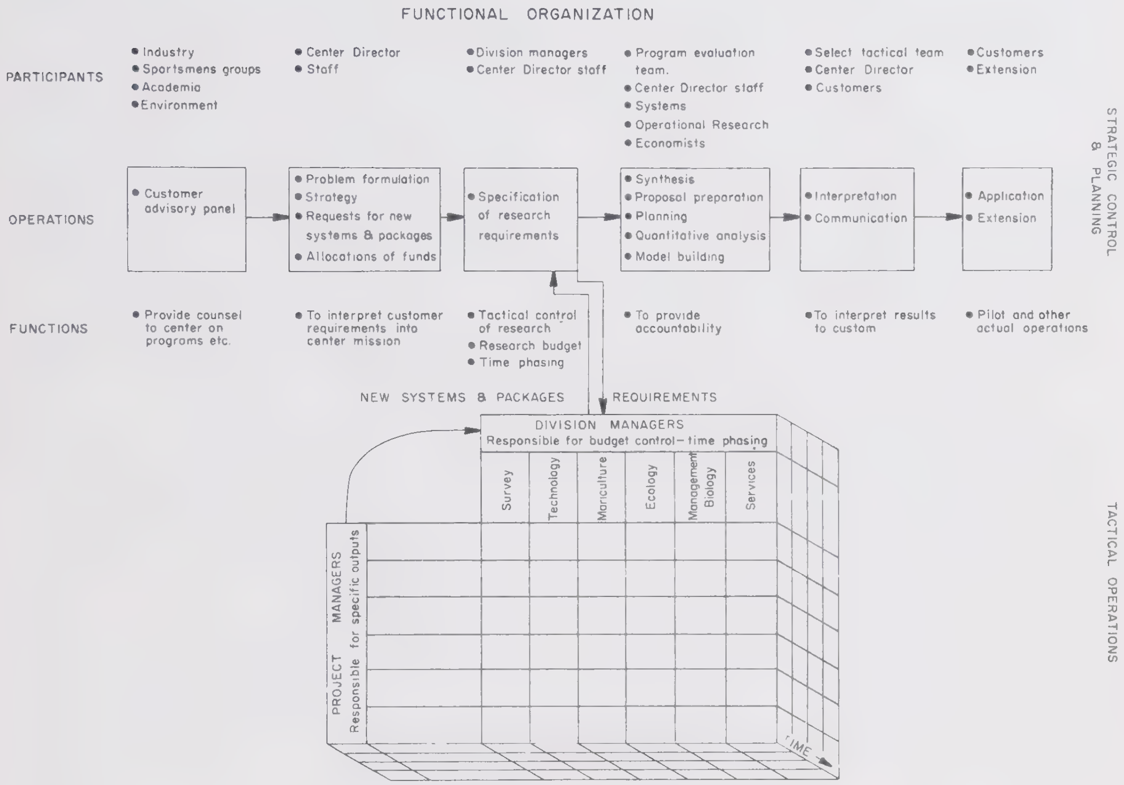
[3] *Appraising Administrative Capability for Development*, p. 10. INTERPLAN Report, Public Administration Division, 1969 (United Nations Sales No. E.69. II.H.2).


FUNCTIONAL ORGANIZATION
PARTICIPANTS
• Industry
• Sportsmens groups
• Academia
• Environment
• Center Director
• Staff
• Division managers
• Center Director staff
• Program evaluation team.
• Center Director staff
• Systems
• Operational Research
• Economists
• Select tactical team
• Center Director
• Customers
• Customers
• Extension
OPERATIONS
• Customer advisory panel
• Problem formulation
• Strategy
• Requests for new systems & packages
• Allocations of funds
• Specification of research requirements
• Synthesis
• Proposal preparation
• Planning
• Quantitative analysis
• Model building
• Interpretation
• Communication
• Application
• Extension
FUNCTIONS
• Provide counsel to center on programs etc.
• To interpret customer requirements into center mission
• Tactical control of research
• Research budget
• Time phasing
• To provide accountability
• To interpret results to custom
• Pilot and other actual operations
NEW SYSTEMS & PACKAGES
REQUIREMENTS
DIVISION MANAGERS
Responsible for budget control – time phasing
Survey
Technology
Mariculture
Ecology
Management Biology
Services
PROJECT MANAGERS
Responsible for specific outputs
TIME
STRATEGIC CONTROL & PLANNING
TACTICAL OPERATIONS

projects, each with a starting and stopping date enabling a shift of personnel among projects rather than keeping specialists within their own more or less narrow disciplines. Such a system is presented in Fig. 2.

Approaches to Strategic Decision

The ninth concept is that if we are to develop responsive institutions, then these institutions will need to be built upon the principles of strategic decision-making as outlined, for example, by Gross (1972). Students of fishery management and of development hold considerable differences in opinion concerning the scope and the nature of appropriate solutions in their respective fields. A common thread does exist, the acknowledgement of the complexity and the need to find simplifications that make solutions more attainable. An important simplification involves decomposing a problem into its strategic and tactical elements and letting the elements of strategy guide the programed tactical decisions. Gross (1972) outlines principles of strategic decision-making that I shall paraphrase and annotate. These are: responsible decision-making, conflict essence of problems, selectivity, total system appreciation, relative proportions, sequential model-using (the art of modelling through), problem interrelations, jointed incrementalism, organized and unorganized interests, the emotional basis of rational action, investment in future capabilities, and power mobilization and use.

Responsible decision-making — The strategic decision-maker has a responsibility to deal directly "with changing patterns of multiple purposes and objectives and handle all relevant variables, including those that may be immeasurable or noncommensurable"; to view one's own decision-making in a matrix of others with possibly conflicting decisions, and to realize that each decision changes the decision environment; to be innovative and to create new values and norms that will elucidate problems that have been previously "swept under the rug" because these did not previously exist, and to "subordinate (without overlooking) technical considerations of both feasibility and consistency to longer range considerations of desirability"; and to generate the most appropriate forms of tactical analysis.

Furthermore, "if tactical, nonresponsible decision-making tends, in the absence of a strategic framework, to dominate the decision-making process, then this may be properly called irresponsible decision-making."

Conflict essence of problems — Conflict is particularly characteristic of fishery resource problems. Owing to the tactical nature of fisheries, it tends to ignore the "identification of the parties at conflict and appraising their strengths and their interests, both apparent and actual" as well as the evaluation of the various "conflict outcomes: avoidance, deadlock, defeat or victory, compromise and integration." It is clear that our decision-making needs to take more explicit account of the conflict essence of problems.

Selectivity — One would think that this simple concept, which advises the decision-maker to examine his alternatives and concentrate upon the best set of alternatives, would be rather generally applied, but "many national planning and development documents are tragic monuments of failure in strategic selectivity. Too often they are built on the double principle of a) stringing together separate plans or programs emanating from every major ministry, or b) providing something for every active pressure group and region. This "laundry list planning" sometimes approaches sheer irresponsibility."

Many fishery programs, whether in developed or developing countries, have the above characteristics. Our fishery institutions tend to be structured in a way that encourages this incremental management approach.

Total system appreciation — Suboptimization is a characteristic of a nontotal system view of a problem. If the complexity of the fishery system is not acknowledged this will lead to suboptimization whereby one element of the system, such as the design and construction of a fish plant, may be optimized but the total system ignored. For example, if the supply of fish is ignored it will be impossible to operate the plant.

Relative proportions — This concept demonstrates the inadequacy of priority lists for making decisions. One simply "cannot order the parts of a system;" thus it is necessary to think in terms of "relative proportions." Inasmuch as many fishery decisions are made on the basis of priorities, the relative proportions concept needs to be considered more often.

Sequential model-using (*the art of modelling through*) — The main point made by Gross is that model building is a scientific endeavor, but model using is an activity employed by decision-makers. Because the model builder often has different objectives than the model user (i.e. the decision-maker), the models produced are usually interesting but not necessarily useful. This reiterates the need for model building to be a sequential iterative process in which the builder interacts with the user so that the model is dynamic rather than static. A good model should mean, not be. Decision-making need not be "muddling through," but it must be "modelling through." Insofar as there are only a limited number of fishery models that actually apply to decision-making, it is difficult to see a widespread applicability of this important technique. This suggests a need for developing additional fishery models.

Problem interrelations — This is another reflection of problem complexity mentioned earlier.

Jointed incrementalism — "A good example is the process of building new development institutions. Thus, in reconstructing an agricultural bank inherited from a colonial period or in building a new institution of this type from scratch, a myriad number of very small, incremental decisions must be made over a rather long period of time. These involve the selection and training of personnel, the mobilization of resources, the development of methods and procedures, the formation of various linkages with farmers, government agencies and other institutions, successive internal reorganizations, etc., etc. If these thousands of steps are pursued on the basis of disjointed incrementalism, the end product is likely to be a rigid institution that operates more like a traditional bank than like a true development agency. Successful institution building is possible only if there is a long-range general model that can serve as a guide to the thousands of incremental decisions. This means jointed incrementalism."

Organized and unorganized interests — The strategic decision-maker needs to consider not only the extent of organized and unorganized interests, but those that will be either organized or unorganized in the future. The strategic decision-maker needs to include within his repertoire the kinds of decisions that can awaken and organize appropriate interests.

The emotional basis of rational action — There are basically two modes of communication, the objective and the emotional. The function of the objective mode is to transmit information, that of the emotional mode to evoke action. The strategic decision-maker must realize that his task most frequently goes beyond simply transmitting information; he needs to elicit action and thus he must develop techniques that utilize an understanding of the emotional basis of rational action.

Investment in future capabilities — In addition to considering investment in terms of the conventional "hard" terms it is necessary to appreciate investment in all areas of management. "a) Investing in people, through education, health, scientific research, and other services or facilities that may make people more productive. b) Investing in the organization and institutions that put hard goods and people together in producing goods and supplying services. c) Investing in the administrative capability that is required to guide organizations and institutions . . . In a certain sense, investing in administrative capability covers all the other aspects of investment, in that administrators – particularly at strategic levels – are directly concerned with continuing decisions on hard goods, people, organizations and other administrators."

Power mobilization and use — The point is made that the strategic decision-maker wants action; plans that do not stimulate action are not particularly useful. The activation of plans involves: "(1) building a support network (or activation base) and (2) the use of various modes of influence (or changing "activation mixes") including persuading, pressuring, and promoting self activation." Gross notes that this is essentially a political process and that politics has been called the art of the possible, but the strategic decision-making in the development area frequently involves intrinsically competing concepts and here we have the art of the improbable.

The above principles are not often considered in fishery management or fisheries strategy. They lie beyond the perimeter of Oddity Land, providing a checklist of items that need to be ticked off before entering the details of a problem in fishery development. Do we consider these items in fishery management and development? How are these items covered in this Conference? What is our philosophy on the strategy of fishery management and development?

Discussion

In discussing the problem of fishery management and development we have assembled a variety of concepts and assertions. The first of these is that there is such a place as Oddity Land. I have never been there, but they tell me that visas are not too difficult to acquire. On the outskirts of Oddity Land they recognize the complexity of the contemporary decision environment and this complexity is characteristic of the decision processes in developing and developed countries. Because of the complexity, advanced informational techniques are needed to analyze alternative means of achieving multiple objectives and developing criteria. Fisheries must then be viewed as systems, and an important simplification of the fishery system is to partition it into its strategic and tactical components. Travellers tell me that in Oddity Land many of the inhabitants consider only questions of tactics and not questions of strategy. Some of the leading citizens do tend to think of doing things the right way, although I understand that one of their number was deported for this. He had thought about responsible decision-making, the conflict essence of problems, selectivity, total system appreciation, relative proportions, sequential model using, problem interrelations, etc.

Now one might think that to make some positive accomplishment in fishery management and development all we need is some system analysis, a dash of operations research, a pinch of social science, etc. Indeed, as Gross notes, these techniques have been to some extent "sold" to developing countries by a variety of foreign governments, international agencies, private companies, special advisors, consulting firms, management institutes, scientists and researchers. But frequently, as Nathaniel Hawthorne noted, "Thus it is that ideas, that grow up within the imagination and appear so lovely to it and of value beyond whatever men call valuable, are exposed to be shattered and annihilated by contact with the practical."

How do we achieve the practical? How do we get away from Gross's cast of characters? "a) The "humble and obedient" civil servant: "I just carry out policies set by the Government . . ."; b) The technical expert: "Let's concentrate on efficiency, and thus release more resources for those humanistic matters . . ."; c) The economic strategist: "We'll be able to enjoy the luxuries of humanism if we tighten our belts today and concentrate our resources in capital investment . . ."; d) The ostrich: "This is not a problem . . ."; e) The dinosaur: "This proves we shouldn't get involved with these fancy new management techniques . . ."

The answer is relatively simple. We need to build new institutions that are capable of facing explicitly the concepts outlined in this paper. These institutions should be chartered to find solutions to practical fisheries problems on a regional scale.

In building these institutions it will be necessary to examine existing fishery arrangements, such as was undertaken by Kasahara and Burke (MS), and also to develop new organizational patterns that help rather than inhibit fisheries organizations in coping with the problems of supply and management in a general development setting. If we do this we may need another conference because the technical questions of fishery management and development do not really explicitly address these questions of strategy. We need to stop describing the present and move dynamically into planning the future.

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7329

THE MORTALITY AND DISPERSAL OF SARDINE EGGS AND LARVAE

By

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INTRODUCTION

The precision and cost of biological sampling in the ocean are jointly determined by the degree to which the organisms to be sampled are heterogeneously distributed temporally, vertically, and horizontally. Oceanic transport and diffusion, behavior, and mortality continuously change the scale and intensity of patchiness: these changes complicate statistical analysis of population size. We are now attempting to describe each of these spatial and temporal characteristics by simple models of mortality and dispersal. It is the purpose of this paper to describe crude estimates of the rates of mortality and dispersal of sardine eggs and larvae.

Ahlstrom (1954b, p. 101–102) held that the mortality rate of Pacific sardines during the embryonic period was negligible. Sample counts from 1940, 1941, 1950, and 1951 indicated that the mortality rate was of the order of 0·5% per day. One large tow was censored from this estimate: if it were included, the summed egg counts would have indicated that 2-day-old eggs were more abundant than 1-day-old eggs by more than 10%. Clearly, this illustrates that conclusions drawn from as many as 50000 eggs taken in 4 years may still be subject to large sampling variability due to patchiness. About 10% of the eggs in the series were from a single haul.

Taft (1960) concluded that sample counts of sardine eggs "were consistent with the hypothesis that the egg population is distributed according to the negative binomial contagious distribution . . . a logarithmic distribution of patch means and a Poisson distribution of eggs within a patch".

The primary technical difficulty with the negative binomial distribution as applied to pelagic eggs is that the number of samples with no eggs has little meaning since "zero samples" can arise from many sources. Zero samples may be drawn by chance from within a patch (with probabilities related to the sampler width), from between patches and, most importantly, from entirely outside the spawning area. The negative binomial distribution admits only the first of these possibilities. Lloyd (1967) discusses the importance of this to the analysis. In the fluid environment of the ocean, dispersal will *increase* the inter-egg distance within the patch and simultaneously *decrease* the distance between adjacent patches: mortality *increases* the distances between eggs within the patch. Eggs of several days' spawning may co-occur in a sample. All that can be said with certainty about the number of samples with no sardine eggs is that the samples were taken where the horizontal space between some adjacent eggs exceeded the width of the plankton net.

The effective egg survey must result in a useful estimate of the total number of eggs present. This is derived in part from an estimate of the number of eggs per unit area, an estimate of the total area covered by spawning, and an estimate of the duration of the spawning period. The number of eggs per unit area will be an underestimate if the major centers of spawning are missed: the total area covered by spawning will be underestimated unless the possibility of zero samples within spawning areas is evaluated. This estimate is clearly related to the size of the sampler and the length of tow.

DEFINITION OF TERMS

Dispersal—the scattering of objects from a small area over a larger area; centrifugal movements (Lloyd, 1967). Not to be confused "with dispersion which in ecological contexts, has the same meaning as pattern" (Pielou, 1969, p. 125): one must be particularly cautious since "over-dispersed" means "patchy" and is defined as a variance: mean ratio significantly greater than one (Skellam, 1952).

Diffusion—the spread of a substance through a medium. The rate of oceanic diffusion is one means used to explain the dispersal of pelagic eggs in this paper. Since I anticipate other modes of dispersal, I choose to use "dispersal" as the effect and "diffusion" as one of the causes.

Transport—the movement of a mass of water and all that it contains from one geographic region to another. Although transport is not a topic of this paper, it is undoubtedly important to the study of egg mortality and distributions (Hirano and Fujimoto, 1969). I define it here merely to discriminate between transport and dispersal. It is conceivable that a group of objects

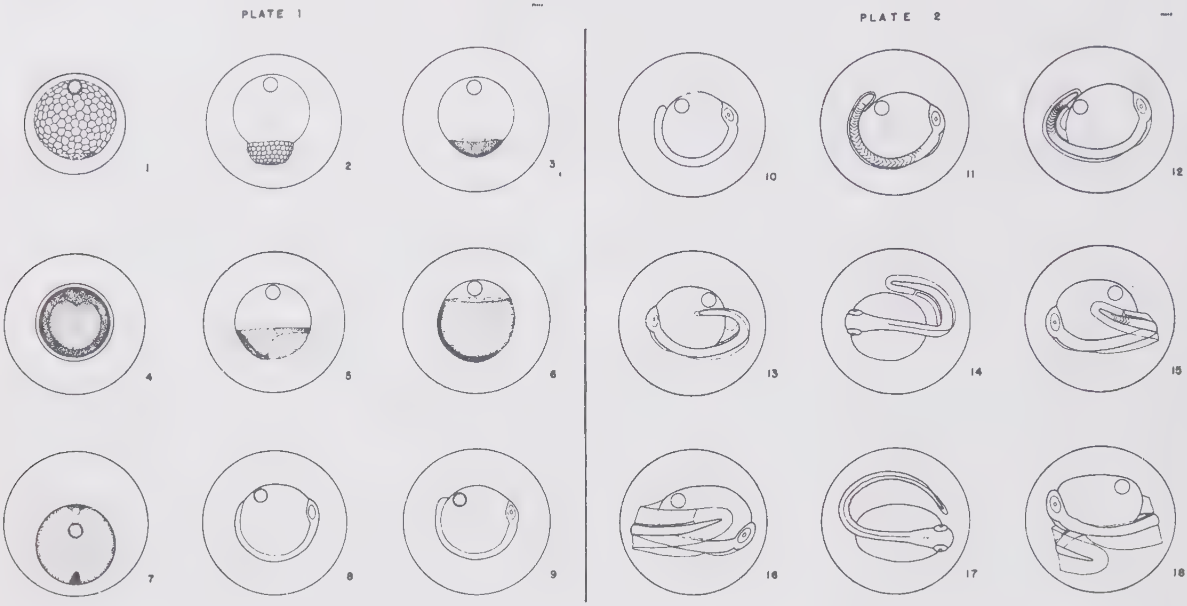

Figure 181. Sardine eggs: (1) stage I; (2) stage II, fairly early; (3) stage II, late; (4) stage III, intermediate, dorsal view; (5) stage IV, beginning; (6) stage V, beginning; (7) stage V, immediately before closing of blastopore, ventral view; (8) stage VI, early; (9) stage VI, late; (10) stage VII, early; (11) stage VII, late; (12) stage VIII, late; (13) stage IX, late; (14) stage X, early, dorsal view; (15) stage X, early; (16) stage XI, early; (17) stage XI, intermediate, dorsal view; (18) stage XI, late. From Ahlstrom 1943.

could retain the same microdistribution while being transported. By dispersal I mean changes in the microdistribution without reference to changes of geographic distribution caused by transport. By microdistribution, I mean the scale of size important to numbers per unit sample; by geographic distribution, I mean the scale of size important to the total distribution of the species and its eggs.

ORIGIN OF DATA

The sardine egg data reported here represents all sardine eggs collected in standard hauls on CalCOFI cruises from January 1951 to December 1959. Approximately 90 cruises were conducted during this period and 14000 standard plankton samples were taken. Of these, 1349 samples yielded about 200000 sardine eggs which have been sorted, staged, assigned a day of spawning and standardized to a unit surface area to correct small differences in towing procedure. Refer to Ahlstrom (1966) for a description of the annual surveys, cruises, and towing techniques.

METHOD OF DETERMINING THE AGE OF SARDINE EGGS

Following the sorting of all sardine eggs from the plankton sample, each egg was characterized as to state of embryonic development and assigned a stage number according to the description and drawings of Ahlstrom (1943). (Plates I and II of that publication are reproduced here as Figure 181 due to the difficulty some may have in obtaining the original).

The original data on the influence of temperature on the rate of development of sardine eggs to four selected stages is reproduced here as Figure 182 (Ahlstrom, 1943). Virtually all eggs are spawned between 2000 and 0400 hours thus the stage of development and the 10 meter temperature (SIO, 1962–1965) collected with each plankton tow may be used to establish the day of spawning. Of the egg counts reported here, those collected between 1951 and 1957 have been published (Ahlstrom, 1953, 1954a, 1958, 1959a; Ahlstrom and Kramer, 1955, 1956, 1957) while those for 1958 and 1959 are not yet published. Eggs collected subsequent to 1959 have been staged but not aged. In Figure 183, I have redrawn the temperature development curves to illustrate the method by which the day of spawning and the hour of sampling can be used to deduce the age of the egg to within about 6 hours. For the purpose of this paper, the time 0 to 2000 hours and the category "Aa" is the 6-hour interval immediately following 2000. Each successive 6 hours is labelled "b", "c", and "d" while the succeeding days are labelled "B", "C", and "D". The numbers used are the total numbers of staged eggs:

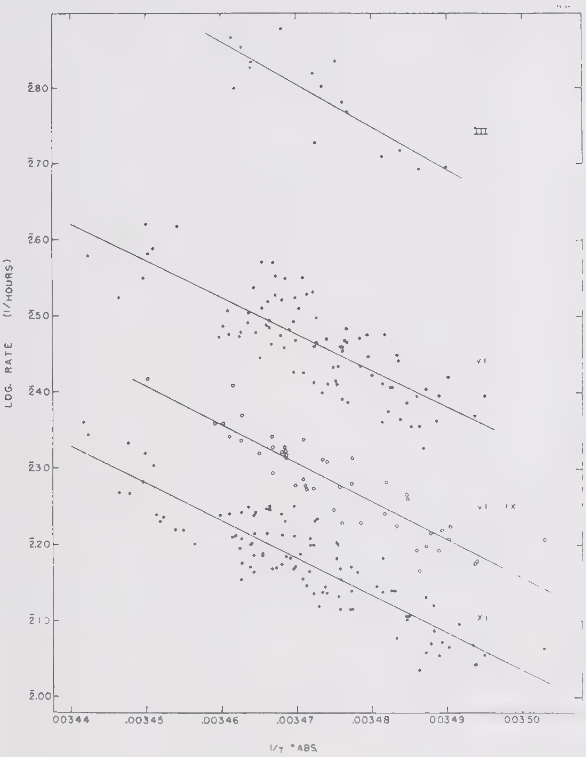

Figure 182. Temperature dependent development rate. (Reproduced without change from Ahlstrom, 1943)

the division into "normal" and "abnormal" categories was ignored since Ahlstrom (personal communication) feels that most abnormalities are due to damage in the net tow, wash down of the samples, and preservation.

The number of eggs in each stage was divided by three so that the numbers represent the number of eggs per 3·33 m² sea surface rather than the number of eggs per 10 m². The standard haul factor used to convert eggs per tow to eggs per 10 m² is normally distributed about 3, thus most sample counts represent the eggs in an oblique net tow under 3·33 m² of sea surface.

RESULTS

Table 101 lists the summaries of egg data by quarter-day intervals from 1951 to 1959. The first half of the table uses as the number of samples, all samples taken which contained any stage sardine egg, in which the accompanying water temperature (10 m) indicated eggs had not yet hatched. The second half of the table includes as the number of samples only those which contain eggs in that stage.

Table 101. Sardine eggs taken on CalCOFI cruises during 1951–59 listed by days. Number per standard haul (number under 3·33 m² sea surface)

	t (days)	Σ_x	Σ_x^2	N	$\bar{x}$	s^2
Total hauls:						
Aa	0·125	4 189	3 029 289	313	13·38	9 529·57
Ab	0·375	25 867	43 721 493	349	74·12	120 127·29
Ac	0·625	29 022	119 479 682	351	82·68	334 514·38
Ad	0·875	20 145	30 532 617	336	59·96	87 536·77
Ba	1·125	27 669	149 045 615	312	88·68	471 356·44
Bb	1·375	20 928	15 843 916	346	60·49	42 255·29
Bc	1·625	23 064	62 303 932	341	67·64	178 658·73
Bd	1·875	18 985	15 434 595	317	59·89	45 245·54
Ca	2·125	8 997	3 408 633	266	33·82	11 714·43
Cb	2·375	8 945	1 975 863	286	31·28	5 951·22
Cc	2·625	14 243	17 966 433	270	52·75	63 996·61
Cd	2·875	6 758	2 801 476	199	33·96	12 989·78
Da	3·125	979	95 875	91	10·76	948·25
Db	3·375	1 310	542 808	53	24·72	9815·94
Dc	3·625	718	174 438	41	17·51	4 046·61
Dd	3·875	65	1 301	13	5·00	81·33
Positive hauls:						
Aa	0·125	4 189	3 029 289	57	73·49	48 597·04
Ab	0·375	25 867	43 721 493	161	160·66	247 284·89
Ac	0·625	29 022	119 479 682	189	153·56	611 825·49
Ad	0·875	20 145	30 532 617	204	98·75	140 607·38
Ba	1·125	27 669	149 045 615	217	127·51	673 692·71
Bb	1·375	20 928	15 843 916	224	93·43	62 280·91
Bc	1·625	23 064	62 303 932	254	90·80	237 982·80
Bd	1·875	18 985	15 434 595	228	83·27	61 029·78
Ca	2·125	8 997	3 408 633	192	46·86	15 638·95
Cb	2·375	8 945	1 975 863	208	43·00	7 686·88
Cc	2·625	14 243	17 966 433	188	75·76	90 306·81
Cd	2·875	6 758	2 801 476	147	45·97	17 060·22
Da	3·125	979	95 875	61	16·05	1 336·05
Db	3·375	1 310	542 808	32	40·94	15 780·00
Dc	3·625	718	174 438	26	27·62	6 184·41
Dd	3·875	65	1 301	8	8·13	110·41

THE EVIDENCE FOR SARDINE EGG MORTALITY

The sample mean in the upper half of Table 101 shows a significant downward trend (rank correlation coefficient $-0{\cdot}8$, $n = 11$) from the second quarter of the first day through the last quarter of the third day. The first quarter of the first day was eliminated due to bias caused by spawning during the period: the last day was eliminated since more than half the stations had been omitted due to hatching temperature. The product-moment correlation coefficient of the sample mean number of eggs and time after hatching is $-0{\cdot}78$ and is significantly different from zero. The

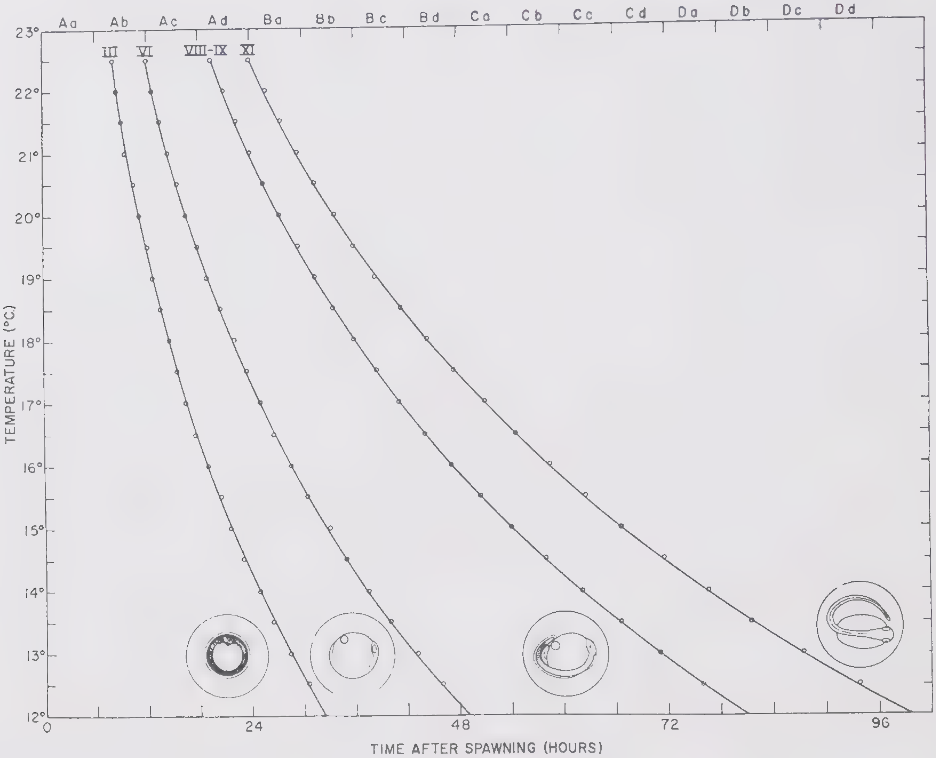

Figure 183. $y = a + bx$ where x is temperature in degrees Celsius, y is the $\log_{10}$ of time in hours and a takes values of 2·22101 (stage III), 2·39977 (stage VI), 2·61754 (stage VIII–IX) and 2·70825 (stage XI). The slope 'b' was the common value, –0·05897. Standard error of estimates 0·03 to 0·04.

strength of these coefficients lends support to the idea that the apparent mortality is not a result of the decidedly non-normal and changing frequency distributions which give rise to the observed arithmetic means.

Further evidence for mortality in the embryonic stages of sardine is given by comparison of the Ahlstrom data from 1950 and 1951 (1954) with his data collected between 1951 and 1959. In Table 102, I have compared the evidence from which Ahlstrom concluded that mortality was negligible to similar data from the years 1951–1959. The elimination of the first 8 hours and the first 6 hours after spawning is justified on the grounds that some spawning is going on during that period: the 2-hour difference between the Ahlstrom (1954b) figures and the ones reported here are regarded as unimportant. In 1950, 82 samples contained sardine eggs at some stage, 4199 eggs were spawned 8 to 32 hours previous to sampling and 4215 were spawned 32·1 to 56 hours previous to sampling. In 24 hours the mean number per standard sample stayed the same (51·20 to 51·40). In the uncensored estimate of 1951 the mean number per standard sample rose from 97·50 (119 samples) to 134·12, a gain of 38% in 24 hours. The censored estimate (by elimination of a single large egg sample) showed a decline from 81·88 (118 samples) to 75·11 per standard haul: down −8% in 24 hours. In the figures for 1951–1959 are included the uncensored totals for 1951, and the mean per standard station changed from 76·19 (1348 samples) to 56·67 (1270 samples) in 24 hours; the mean density at any time may be estimated from these two points, as follows: —

$$N_t = N_0 \exp(-Z_t)$$
$$N_t = 95{\cdot}15 \exp(-0{\cdot}2956t)$$

where N_t is the mean density of eggs in number per 3·33 m² at time t
N_0 is the mean density of eggs at time zero
Z is the instantaneous mortality rate per day
t is the time in days.

It is important that the absolute difference in the total number of eggs is greater than any single (102 703 to

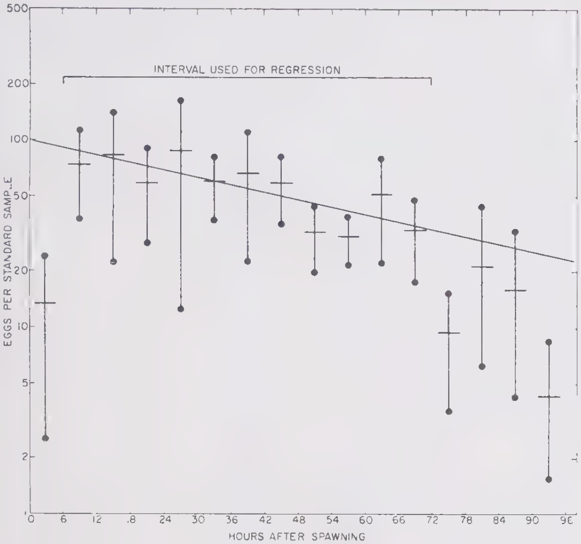

Figure 184. Sample means and an estimate of the 95% fiducial limits [$\pm 1{\cdot}96\, s/\surd(n)$] for all samples which contain any stage sardine egg, 1951–59. (Table 101). The line is a least squares fit to the log of sample means from 6 to 72 hours. Time zero is 2000 hours.

71974) sample (maximum sample, 1959–1959, 10333 eggs per standard sample).

It seems likely from the above that significant mortality does occur in the embryonic stage. Because the rate is determined from only two points, the rate of 0·3 per day is not to be taken as an accurate slope. To gain a sense of the crude mortality rate, I have plotted the sample means and an estimate of the 95% confidence limits, for each of the 16 categories, in Figure 184. The formula for the curve is (11 points, Ab–Cd)

$$N_t = 94{\cdot}02 \exp(-\ 0{\cdot}3074)$$

This rate of mortality, 0·3074 per day over 3 days, does not differ markedly from the 0·2956 of the first 2 days of fully recruited eggs (Table 102): the standard error for the mortality rate derived from two points is not evaluable but for the 11 point curve the standard error is 0·087 (for method of fitting line and determining standard error see Conway, Glass and Wilcox, 1970).

THE EVIDENCE FOR SARDINE EGG DISPERSAL

The importance of dispersal was first indicated by the increased proportion of positive egg samples with time (Table 103, Fig. 185) after spawning. Other evidence includes a) the rate of decline in the mean number of eggs per positive sample exceeds the mortality rate (Table 101, Fig. 186); b) the change with time of the frequency distribution of mean distance between nearest neighbor eggs while the frequency distribution of eggs per sample remains relatively stable (Fig. 187); c) the decline in the Lloyd (1967) "patchiness" (Table 105) ratio; and d) the decrease with time of the probability of obtaining a "large" sample of eggs (Tables 104, 106).

Table 102. Comparison of crude sardine egg mortality estimates

Period	Age	Number of eggs	Number of stations[1]	Mean	Percent difference
1950	8–32 hr.	4199	82	51·20	–
	32·1–56	4215	–	51·40	–
1951	8–32 hr.	11602	119	97·50	–
Uncensored	32·1–56	15960	–	134·12	+38%
1951	8–32 hr.	9662	118	81·88	–
Censored	32·1–56	8863	–	75·11	– 8%
1951–59	6–29 hr.	102703	1348	76·19	–
	30–54	71974	1270[2]	56·67	–26%

[1] Number of stations with any stage sardine egg.

[2] 78 stations removed from consideration since eggs would not be anticipated at that temperature due to hatching.

The rate of dispersal for sardine egg patches for the first day after spawning is reflected by the change in proportion of samples which are positive, given by:

$$P_d = 38{\cdot}05t^{0{\cdot}2332}$$

where P_d is the proportion of samples which are positive, and t is the time in days.

Table 103 shows that the proportion of samples which are positive stabilizes after a day and a half and I presume that this is due to the development of spaces between eggs such that a sampler may pass between eggs in a patch. The dispersal rate is clearly distinguishable from the increased probability of positive samples due to spawning (Early, Table 103) immediately after 2000 hours (Fig. 185):

$$P_s - 6{\cdot}08t^{3{\cdot}1223}$$

where P_s is the percent positive samples in the first 7 hours of spawning.

The decline in the mean number of eggs per positive sample is at a higher rate than could be explained by mortality alone (Table 101, Fig. 186):

$$N_{t+} = 194{\cdot}13 \exp(-\ 0{\cdot}5038t)$$

where N_{t+} is the sample mean number of eggs per positive sample per 3·33 m^2 surface area.

Table 103. Percentage of samples positive for sardine eggs taken on CalCOFI cruises during 1951–59, listed by days

	t (days)	Number of samples	Number of positive samples	Percent positive samples	Confidence limits (%)
Aa	0·125	313	57	18	±4
Ab	0·375	349	161	46	5
Ac	0·625	351	189	54	5
Ad	0·875	336	204	61	5
Ba	1·125	312	217	70	5
Bb	1·375	346	224	65	5
Bc	1·625	341	254	74	5
Bd	1·875	317	228	72	5
Ca	2·125	266	192	72	5
Cb	2·375	286	208	73	5
Cc	2·625	270	188	70	5
Cd	2·875	199	147	74	6
Da	3·125	91	61	67	10
Db	3·375	53	32	60	13
Dc	3·625	41	26	63	15
Dd	3·875	13	8	62	28
Samples within the first 9 hours					
1 hr.	0·042	106	7	7	5
3 „	0·125	105	19	18	7
5 „	0·208	102	31	30	9
7 „	0·292	109	48	44	9
9 „	0·375	123	56	46	9

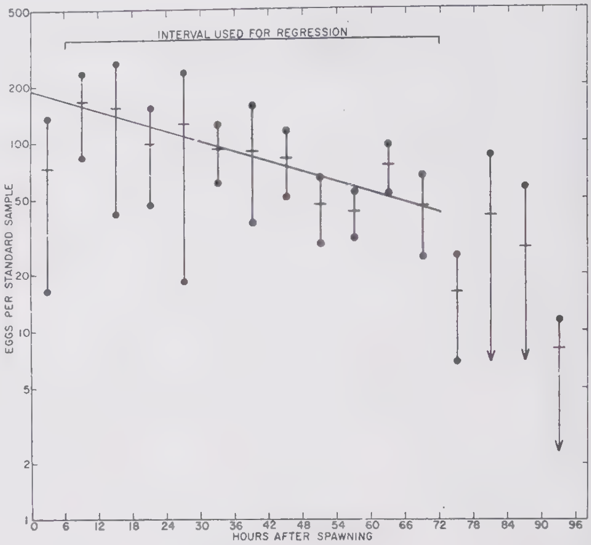

Figure 186. Sample means and an estimate of the 95% fiducial limits [$+1{\cdot}96\, s/\sqrt{(n)}$] for all samples positive for that particular stage age, 1951–59. (Table 101, positive samples). The line is the least squares fit to the $\log_{10}$ of sample means from 6 to 72 hours, time zero is 2000 hours.

The rate of $-0{\cdot}5038$ (S. E. 0·075) per day exceeds the mortality rate (0·3074; S. E. 0·087). The difference is explained by the fact that the rate of dispersal exceeds the rate of aggregation, if any (such as surface convective cells) exists.

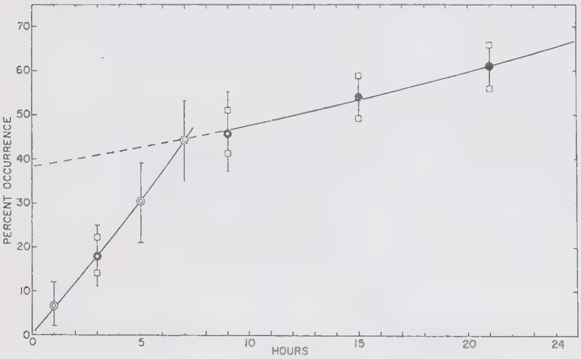

Figure 185. The percent occurrence of sardine eggs in the day of spawning. Solid circles are the percent occurrence of 6 hour intervals plus an estimate of the 95% fiducial limits [$+1{\cdot}96\sqrt{(pq/n-1)}$ squares]. Open circles are the percent occurrence of sardine eggs in 2 hour intervals and an estimate of the 95% limits (bars). The dashed line is the extension of the least squares estimate of $\log_{10}$ percent occurrence on time between 6 and 30 hours. The solid line near the origin (2000 hours) is the least squares estimate of the percent occurrence over the first eight hours.

The characteristic of Pacific sardine egg patchiness is that most eggs occur in a few large samples (Tables 104, 106). Most positive samples contain relatively few eggs. A rule-of-thumb for this species is that 90% of the eggs occur in about 10% of the positive samples. The results of 349 samples taken between the hours of 0200 and 0800 are shown in Figure 187. The summary of the three stages of eggs taken in these samples (Ab, Bb, Cb)—Table 101 — shows the change of the sample mean number per standard sample to be 74, 60, and 31 eggs (regression estimate 86, 61, and 43 eggs respectively) at 24 hour intervals. While the number of eggs per sample changes gradually and retains the same form (b) the frequency distribution of percent of eggs (a) shifts from mean nearest neighboring category, of less than 2·5 cm, to the 5 cm category.

Lloyd (1967) proposed the following measure of "mean crowding", which is the number of other individuals per quadrat per individual:—

$$\overset{*}{m} = \sum_{i=1}^{N} x_i/N \tag{6}$$

where $\overset{*}{m}$ = population estimate of mean crowding

N = number of individuals

x_i = number of other individuals that are located with the individual in the same quadrat.

Table 104. Frequency distribution of samples of sardine eggs taken on CalCOFI cruises, 1951–59, by mean space between nearest neighbors and mean number per standard sample. (Number under 3·33 m² sea surface)

Mean space between nearest neighbors	Eggs/sample	Aa	Ab	Ac	Ad	Ba	Bb	Bc	Bd	Ca	Cb	Cc	Cd	Da	Db	Dc	Dd	Total
1 cm	3705–33333	0	1	1	0	2	0	1	0	0	0	1	0	0	0	0	0	6
2	1334–3704	1	5	4	3	0	2	1	2	0	0	0	0	0	0	0	0	18
3	681–1333	1	4	2	0	1	6	3	4	2	0	1	1	0	1	0	0	26
4	413–680	1	5	6	8	5	7	4	7	3	2	5	3	0	0	0	0	56
5	276–412	2	3	6	4	3	3	6	6	3	5	4	2	0	0	1	0	48
6	198–275	1	7	6	4	9	7	7	3	3	6	4	3	1	0	0	0	61
7	149–197	0	2	6	3	6	3	3	8	2	8	6	4	0	0	0	0	51
8	116–148	1	3	5	7	1	9	3	7	3	5	4	5	0	2	1	0	56
9	93–115	0	3	4	7	3	9	8	3	4	6	2	0	0	1	0	0	50
10	77–92	1	5	3	6	3	3	9	4	3	1	11	4	1	1	0	0	55
11	64–76	1	4	3	4	5	6	2	4	4	2	3	2	1	0	0	0	41
12	54–63	1	2	1	3	8	4	8	4	9	5	6	1	1	0	1	0	54
13	47–53	1	3	5	1	2	3	5	8	3	4	2	3	1	0	0	0	41
14	41–46	0	4	2	7	4	8	7	2	3	5	5	1	0	0	0	0	48
15	36–40	0	5	2	2	5	2	6	4	4	1	3	0	0	0	0	0	34
16	32–35	0	5	2	5	3	4	3	2	2	3	2	2	0	0	0	0	33
17	28–31	1	1	3	1	4	3	5	2	5	6	3	1	1	1	1	1	39
18	25–27	0	2	2	6	3	3	1	1	4	5	2	3	2	0	0	0	34
19	23–24	0	2	3	1	5	2	1	5	2	2	4	1	0	0	2	0	30
20	21–22	1	1	5	3	3	2	5	2	1	4	2	2	3	0	0	0	34
21	19–20	1	2	2	3	1	1	2	4	3	2	3	1	3	1	0	0	29
22	17–18	1	2	4	5	2	4	5	3	4	2	5	0	1	0	0	0	38
22·5–23·1	16	2	0	3	4	3	1	2	2	1	1	1	1	2	1	0	0	24
23·2–23·9	15	1	0	2	1	1	3	1	0	2	2	1	4	2	0	0	1	21
24·0–24·7	14	0	2	3	0	1	2	3	5	5	2	1	2	0	0	0	0	26
24·8–25·7	13	0	0	3	0	3	1	6	4	3	3	2	5	1	0	0	0	31
25·8–26·8	12	1	1	2	4	5	2	7	0	4	6	5	1	0	1	0	0	39
26·9–28·1	11	1	0	4	2	3	3	3	4	2	2	2	2	1	0	1	0	30
28·2–29·5	10	3	3	1	3	2	5	3	3	3	6	3	3	2	0	0	0	40
29·6–31·2	9	0	4	8	5	5	2	2	5	10	6	2	3	2	1	0	1	56
31·3–33·2	8	1	7	3	4	3	4	3	2	5	7	1	6	4	1	0	0	51
33·3–35·7	7	1	4	5	6	6	3	8	6	10	4	8	2	0	0	0	0	63
35·8–38·8	6	2	1	6	5	5	9	6	8	3	2	3	2	3	2	0	0	57
38·9–42·9	5	2	5	2	7	6	5	12	8	6	3	7	7	1	3	2	0	76
43·0–48·7	4	5	7	6	10	12	11	6	11	9	10	10	7	3	2	2	0	111
48·8–57·6	3	6	9	6	14	15	16	17	16	12	14	14	13	3	3	2	2	162
57·7–74·4	2	5	17	22	12	17	19	22	21	16	28	13	15	9	4	2	1	223
74·5–129·0	1	12	30	36	44	52	47	58	48	34	38	37	35	13	7	11	2	504
129·1 – Infinity	0	256	188	162	132	95	122	87	89	74	78	82	52	30	21	15	5	1488
Total		313	349	351	336	312	346	341	317	266	286	270	199	91	53	41	13	3884

The sample estimate was calculated by the formula:

$$\overset{*}{x} = \bar{x}[(s^2/\bar{x}) - 1] \qquad (7)$$

The ratio of the sample estimate for mean crowding $\overset{*}{x}$ and the sample estimate of the mean is equivalent to the reciprocal of the negative binomial k and is described by Lloyd (loc. cit.) as a measure of "how many times as 'crowded' an individual is on the average, as it would have to be if the same population had a random distribution". "Patchiness" declines with time (rank difference correlation coefficient = $-0{\cdot}4, n = 16$).

Even though the periphery of the egg patches spreads rapidly, most eggs remain closely spaced near the origins of the patches (discounting transport). Table 106 lists the 24 largest samples of the 9-year series. The list includes all samples where the mean horizontal space between nearest neighbors was less than 2·5 cm. Although these 24 samples represent only 0·6% of the samples taken, they contained 37·5% of the eggs. There is no obvious order of rank and age, thus the absolute size of these samples appears to be due to chance. The probability of obtaining these samples does change with time, however:

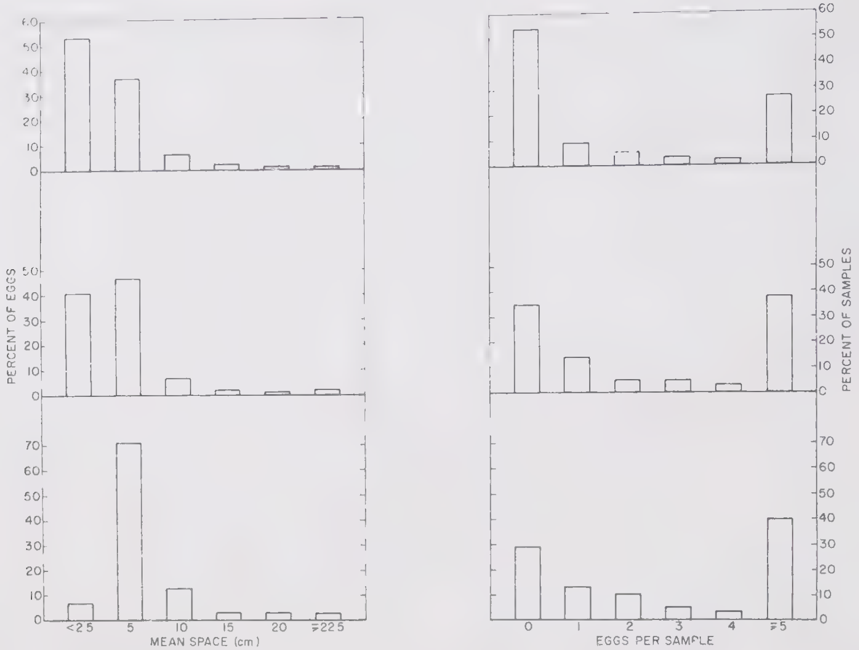

Figure 187. Frequency distribution of eggs (a) and samples (b) at 9·33 and 57 hours after spawning. Part "a" is the percent of the eggs in each mean space category (mean space equivalents in numbers per m² in Table 104). Part "b" is the percent of samples in "eggs per sample" categories.

Table 105. Estimate of mean crowding of sardine eggs taken on CalCOFI cruises during 1951–59, listed by days

	Time t	Mean density $\bar{x}$	Variance s^2	Variance /mean $s^2/\bar{x}$	Mean crowding $\overset{*}{x}$	Patchiness rates $\overset{*}{x}/\bar{x}$
Aa	0·125	13·38	9529·57	712·22	724·60	54·16
Ab	0·375	74·12	120127·29	1620·71	1693·83	22·85
Ac	0·625	82·68	334514·38	4045·89	4127·57	49·92
Ad	0·875	59·96	87536·76	1459·92	1518·88	25·33
Ba	1·125	88·68	471356·44	5315·25	5402·93	60·93
Bb	1·375	60·49	42255·29	698·55	758·04	12·53
Bc	1·625	67·64	178658·73	2641·32	2707·96	40·03
Bd	1·875	59·89	45245·54	755·48	814·37	13·60
Ca	2·125	33·82	11714·43	346·38	379·20	11·21
Cb	2·375	31·28	5951·22	190·26	220·54	7·05
Cc	2·625	52·75	63996·61	1213·21	1264·96	23·98
Cd	2·875	33·96	12989·78	382·50	415·46	12·23
Da	3·125	10·76	948·25	88·13	97·89	9·10
Db	3·375	24·72	9815·94	397·08	420·80	17·02
Dc	3·625	17·51	4046·61	231·10	247·61	14·14
Dd	3·875	5·00	81·33	16·27	20·27	4·06

Table 106. Large samples of sardine eggs 1951–1959

Rank	Density (number/sample)	Age	
1	10333	Ba	1·125 days
2	10204	Ac	0·625 ,,
3	7097	Bc	1·625 ,,
4	6665	Ba	1·125 ,,
5	4077	Ab	0·375 ,,
6	3854	Cc	2·625 ,,
7	3610	Ad	0·875 ,,
8	3163	Ab	0·375 ,,
9	2797	Ad	0·875 ,,
10	2654	Bc	1·625 ,,
11	2507	Ad	0·875 ,,
12	2479	Bd	1·875 ,,
13	2206	Ab	0·375 ,,
14	2190	Bb	1·375 ,,
15	1940	Ac	0·625 ,,
16	1800	Bd	1·875 ,,
17	1699	Ac	0·625 ,,
18	1698	Bb	1·375 ,,
19	1504	Ac	0·625 ,,
20	1481	Ab	0·375 ,,
21	1453	Ab	0·375 ,,
22	1363	Ac	0·625 ,,
23	1352	Aa	0·125 ,,
24	1348	Ab	0·375 ,,

Day	$\underline{\underline{N}}$	N_+	%
0·5	11	350	3·1
1·0	5	421	1·2
1·5	4	478	0·8
2·0	2	420	0·5
2·5	1	396	0·3

where Day is the time in days after spawning,

$\underline{\underline{N}}$ is the number of large samples (> 1333 per standard sample)

N_+ is the number of positive samples

% is the percent of positive samples which are large.

Table 104 indicates that the large samples are part of a continuous distribution in sample sizes.

Considerations of oceanic diffusivity (Okubo, 1968) would suggest that the smaller the scale of the patch, the slower would be the rate of diffusion. Okubo has fitted a curve to existing diffusion experiments and the following formula describes the scale dependent effect:

$$Ka = 0{\cdot}0103L^{1{\cdot}19}$$

where Ka = the apparent diffusivity in $\text{cm}^2\ \text{sec}^{-1}$

L = the scale of the patch in cm.

By use of the rate of increase of positive stations (Smith, MS.) in Table 103, the scale of patch involved in the dispersal of sardine eggs appears to be of the order of 10's to 100's of meters patch diameter. One can say with reasonable certainty, that the scale of diffusion which affects the dispersion of sardine egg numbers per unit area and is the major source of variance, is not the sort that one would expect from the spawning of single or small groups of females nor that expected by the spawning of huge shoals of fish schools over kilometers and 10's of kilometers.

THE MORTALITY AND DISPERSAL OF SARDINE LARVAE

We have attempted in a preliminary way to align larval and egg time series to days after spawning as corrected by hatching and yolk sac growth by temperature. A series of all 171 samples in 1955 indicates that larval apparent mortality increases somewhat immediately after hatching, but most changes can be attributed to escapement through the meshes of the net (Ahlstrom, 1954b):

1955	day	$\bar{x}_r$	$\bar{x}_e$	$\%_e$
	3	32·56	32·56	
	4	23·11	11·42	65 %
	5	16·41	6·31	45 %
	6	11·65	3·79	40 %

where $\bar{x}_r$ = predicted value at 29% per day

$\bar{x}_e$ = measured value

$\%_e$ = estimated rate.

Lenarz (this vol.) estimates the overall larval mortality rate at approximately 0·1 per day. We anticipate that extensions of this technique and new laboratory rearing data will allow improvements for this estimate. There is no apparent difference in the rate of dispersal of early larvae as compared to eggs. Patchiness exists for the individual larva through at least the 7th day: for the 1955 data, more than 3/4 of the larvae were spaced less than 20 cm from the mean nearest neighbor.

DISCUSSION

Although the main objective of this paper was to use the observed distributions of sardine eggs at differing ages to improve the precision of biological sampling and analysis per unit cost, there are important leads in these results for the study of sardine mortality and pelagic ecology in general. Following the discussion on sampling in the presence of patchiness and dispersal, I will briefly relate the dispersal and mortality of sardine eggs and larvae to oceanic conditions of life.

SAMPLING AND ANALYSIS

The general finding of this paper is that sardine eggs are spawned in a mosaic pattern of fish school proportions, and the eggs at the perimeter subsequently disperse to a condition of randomness in a large "corona" around a concentrated "centrum". The size of the centrum appears to be of the order of 10's of meters diameter while the size of the "corona" rapidly shifts from one to several hundred meters after spawning. Horizontal mean space between nearest neighbor eggs is of the order of 1 or 2 cm at spawning and changes to 15 to 20 cm mean space between most, several-day old larvae.

The implications for sampling strategy at sea are clear. Large numbers of small samples, each covering a unit square metre will rapidly yield a catch size distribution which defines the amount of open area between patches in a spawning area, the mean density of the randomly placed eggs in the "corona" and a sample estimate of the negative binomial k. It seems likely that samples of this kind will not yield useful rates of such gradual phenomena as mortality until a thousand or so positive samples have been taken. Considering the relative sizes of the "corona" and "centrum" no practical tow length could be envisaged which would be long enough to stabilize the variance mean ratio at unity. Larger scales of "patchiness", such as groups of schools of spawning adults, may well defeat the purpose of lengthening the tow.

Some statistical purpose would be served by making "zero" tows less likely. The 30 to 40% of the spawning area which appears to be free of eggs in 3·33 m² samples might have only 5 to 10% negative tows with 10 m² samples. Certainly this would reduce the "zero" labelling of an 8000 square mile area represented by a single negative tow in a spawning area.

In the analysis of egg concentrations, I can see no useful analytical purpose in contouring discontinuous distributions of egg counts for single stations as suggested by Sette and Ahlstrom (1948). The scale of patchiness suggested by these data would cause local fluctuations of several orders of magnitude between adjacent stations, and the assumption of contour continuity would not hold.

SARDINE MORTALITY IN THE EMBRYONIC STAGE

The daily rate of $-0{\cdot}31$ for sardine egg mortality is unexpectedly high. Comparison with the negligible rate held by Ahlstrom (1954) by similar techniques, yields a 26 per cent change in the first two fully recruited days. I conclude that the egg mortality rate of $-0{\cdot}31$ (S.E. 0·087) is demonstrably higher than the 0·1 per day rate postulated by Lenarz (this vol.) for sardine larvae. Both egg and larval mortality rates depend on the assumption that station temperatures at 10 m depth are representative of the actual temperature of development. We are now beginning a study of temperatures throughout the upper mixed layer for an estimate of the possible magnitude of error in this assumption. Marr (1956) proposes three mortality rate curve types for early stages. I believe that the crude rates of mortality derived here support his "type two" curve and gradually change from 0·3 to 0·1 per day in the first few weeks of life. Further studies and samples are obviously needed on this point, however. Intuitively, I feel that the "critical" period type curve if occurring should have been more obvious from the extensive set of data.

ECOLOGICAL CONSIDERATIONS OF DISPERSAL AND MORTALITY

The universal nature of patchiness in pelagic invertebrates (Clutter, 1969) and fish eggs and larvae tempts one to speculate that the "mean crowding" elucidated by Lloyd (1967) should be considered as an index of "mean adaptive aggregation" for pelagic animals. Among the adaptive properties of patchiness for larval fish is the rate at which the subsequent behaviour and schooling may develop from chance contacts (Breder, 1967; Shaw, 1963). Van Olst and Hunter (1970) find that interfish distances of anchovy larvae in the laboratory close rapidly from three body lengths spacing at 30 mm length to less than one body length space at 70 mm length. The ontogeny of these reactions to other fish must be affected by dispersal rates encountered during the planktonic stage.

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EFFECT OF ANTIBIOTICS ON SURVIVAL OF CARANGID FISH LARVAE *(Caranx mate)*, REARED IN THE LABORATORY*

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Techniques are described which have proved successful in rearing the larvae of nine species of marine fishes in Hawaii. The results of intensive experiments on larvae of the carangid fish, *Caranx mate*, are presented, with emphasis on the effects of various antibiotics on bacterial populations in rearing containers and on larval survival. Microcopepods, gastropod veligers, and rotifers were found to be suitable foods for *C. mate* larvae, and larval survival was enhanced when the phytoplankter *Chlorella* was added to cultures. Four bacterial genera were identified from natural water samples and from rearing containers in culture situations. *Pseudomonas* was the most abundant genus, *Cytophaga* next most abundant, followed by *Vibrio; Flavobacterium* was identified but uncommon. uncommon.

In sea water containing low initial numbers of bacteria, bacteria increased more rapidly and stabilized at a higher density than in sea water containing higher initial densities. Of a number of antibiotics tested, the most effective in decreasing bacteria in sea water and enhancing hatching success and larval survival were the polymyxins, penicillins, and especially erythromycin. Repeated treatments with the same antibiotic on day 3 of the experiment did not reduce bacterial density or improve larval survival, when compared with a single treatment on day 1. These results are discussed in relation to the mode of action of the antibiotics, and suggestions are made concerning profitable lines of future research.

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INTRODUCTION

Concomitant with increasing attention to marine research and aquaculture has been the interest in techniques for rearing marine larvae, particularly of commercially valuable species. Several marine fish larvae have been reared successfully in the laboratory, especially within the families Clupeidae (e.g. Blaxter, 1962) and Pleuronectidae (Shelbourne, 1964). May (1971) summarizes most attempts to raise marine fish larvae from 1878 through 1969.

Considerable research has been conducted on the aquaculture of fishes belonging to family Carangidae, primarily the pompano (*Trachinotus carolinus*; Fields, 1962; Berry and Iversen, 1967; Moe *et al.*, 1968; Finucane, 1969; Bellinger and Avault, 1970) and the yellowtail (*Seriola quinqueradiata*; Inoue and Tanaka, 1966; Tamura, 1970). The pompano is being reared successfully by private aquaculture concerns although the techniques are not available to the public. Several investigators at the University of Miami have reared a number of tropical marine fish species (e.g. see Houde and Palko, 1970 for techniques) including several species of Carangidae (Charles Mayo, unpublished).

In Hawaii, the carangid *Caranx mate* (= *Atule mate* [Cuvier in Cuvier and Valenciennes] 1883; see Williams, 1958) or omaka is a highly-prized food fish exhibiting similar aquaculture potential. This paper reports results of experiments in which *C. mate* larvae were reared to juveniles. The larval rearing techniques used with this fish were found applicable to other carangids and a few species of other families. We hope that our results can be applied to rearing of other semi-tropical or tropical fish.

Bacteria and food appear to be the most important environmental variables during early development in the laboratory. Two high mortality periods usually occur in early development; (1) at time of hatching and (2) when yolk is completely catabolized and larvae must begin to feed. We found, as did Oppenheimer (1955), that bacteria affect hatching of eggs and that by controlling bacteria with antibiotics, percent hatching is significantly increased. Our initial research has been concentrated on the effect of certain antibiotics. The importance of providing appropriate type and concentration of food to meet energy requirements of larvae during the crititical stage after yolk is catabolized has been demonstrated in several studies (*e.g.* Lasker, 1962, 1965; Lasker *et al.*, 1970). A comprehensive summary of experiments in the feeding of larval fishes is given by May (1970).

This paper includes a description of our larval rearing techniques, general life history and early development of *C. mate*, and results of experiments testing the effects of different types of food, bacteria and antibiotics on hatching and survival of *C. mate* larvae. The growth of cultured *C. mate* from egg to adult was reported by Watarai (1973). Detailed descriptions of the embryonic and larval development are being prepared by Miller (ms. in prep.) and additional studies of larval energetics and the effects of temperature, salinity, and food are in progress.

REARING METHODS

The rearing technique outlined below was delineated through a series of multiple factor experiments testing various ranges of variables. Where significant differences are referred to in the results, significance occurs at least at the $P < 0.05$ level. Analyses were performed on a time-sharing computer facility using standard BASIC programs for the statistical techniques of analysis of variance, covariance and regression. The rearing techniques are similar to those used by others in rearing invertebrate larvae (e.g. Loosanoff and Davis, 1963) and fish larvae (e.g. Schumann, in Bardach, 1968; Lasker *et al.*, 1970; Houde and Palko, 1970). Most of our experiments were performed with *C. mate* eggs and larvae. A list of other species also reared with this technique is in Table 1. Small volumes of

TABLE 1

Species of fish reared by described technique at 25 °C and 34–36‰.

Scientific name (Gosline and Brock, 1965)	Common name
Dussumieriidae	
Etrumeus micropus	Herring
Engraulidae	
Stolephorus purpureus	Anchovy
Mugilidae	
Mugil cephalus	Mullet
Apogonidae	
Apogon brachygramma	Cardinal Fish
Carangidae	
Gnathanodon speciosus	Jack
Caranx mate	Jack
Pomacentridae	
Abudefduf sordidus	Damselfish
Abudefduf abdominalis	Damselfish
Tetraodontidae	
Unknown species	Puffer

water in a closed system were used so that quantitative data could be collected. A modification of these techniques to larger volumes of water, usually correspondingly increased survival. Under the conditions below, percent survival of carangid larvae through critical stages to 2 weeks from hatching varied from 1–80%, averaging 40%. Mortality of larvae after 14 days was negligible.

Collection of Eggs

For most experiments, fertilized eggs of *C. mate* were collected from the southern sector of Kaneohe Bay in surface tows with a 1-meter plankton net (303 μ mesh). Immediately after collection, samples were diluted in buckets and aerated. At the Hawaii Institute of Marine Biology Laboratory on Coconut Island in Kaneohe Bay, samples were passed through sieves to remove extraneous plankton. Eggs were concentrated, washed in sterile sea water and resuspended in a few liters of sea water. Eggs were then sorted by hand into beakers of sterilized sea water. The eggs when collected vary in size from 690–750 μ maximum dimension, with a mean of about 720 μ. In this paper, ‘day 1’ refers to the day on which each experiment was begun, usually corresponding to the day after the eggs were fertilized; subsequent days are numbered accordingly.

Artificial Fertilization of Eggs

In some experiments, ripe females were stripped by hand and eggs collected in glass bowls without sea water (dry fertilization). Sperm from a ripe male was mixed with eggs and the mixture allowed to stand 3–4 min. Fertilized eggs were concentrated in a sieve, washed 5–10 min with sterile sea water and resuspended. The remainder of the procedure was similar to that above. A maximum of 60% fertilization was achieved by this method. Survival was poor, however, and for most experiments described below planktonic eggs were used.

Rearing Containers

For most experiments, straight-sided polyethylene ‘utility tubs’ (21.6 cm height × 31.7 cm diameter) were used. The tubs were green (Webster International Dictionary, 2nd ed., 1957, p. 540; Color #58, chart B. Chromium Green) and were filled with 12 l of sea water. Covers were made of 1/8 in plexiglass, approximately 36 cm in diameter with a small hole drilled in the center for an air tube.

Filtration

Sea water was filtered through a series of three cellulose Cuno filters (Aquapure water filters; cartridge No. P110; Cuno Engineering Corporation, Meridian, Conn.). The three Cuno filters effectively removed most organisms from the sea water, including most bacteria. Best results were obtained when new filters were used daily.

Sterilization

Filtered water was passed through a unit containing ultraviolet germicidal lamps (G.E.). All apparatus was also sterilized by irradiating under germicidal lamps for approximately 15 min.

Aeration

Water in containers was *gently* aerated by means of a l-ml disposable pipette placed through the center of the cover and attached to an air pump. Oxygen was monitored in the containers daily and adjustment of the oxygen concentration was made to maintain oxygen at saturation level. Considerable care was exercised to avoid bubbling or moving water too violently, or mortality was greatly increased.

Temperature and Salinity

Most experiments were performed within a temperature range of 23–25°C and salinity range of 34–36‰.

Light

Continuous light was provided uniformly over the surface of containers using G.E. Cool-white and Daylight 40-watt fluorescent bulbs. Light intensity varied from approximately 200–500 ft-c (2160–5400 lux*). A high light intensity was necessary to maintain normal phytoplankton growth in cultures and for optimal feeding of fish larvae.

Antibiotics

Several antibiotics were tested (Table 6). Sea water was treated with antibiotics before eggs were added.

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* 1 lux (lx) = 1 lumen per square meter.

Larval Concentration

100 eggs/12 l sea water (1 egg/120 ml; 8.3 eggs/liter).

Food Type

Wild zooplankton

This consisted primarily of microcopepods; *Oithona simplex, O. nana* and *Paracalanus* sp. (Edwin Bartholomew, pers. comm.). Plankton was collected using a night-light and small centrifugal pump attached to a timer. After plankton had been attracted to the light for 2 h prior to sunrise, the water pump switched on, transferring plankton from the collection net into another aerated, 73-μ net. The plankton was washed with sterile sea water and sorted into size groups using a series of sieves with different mesh size. Plankton normally fed to larvae from days 2–12 was approximately 73–150 μ maximum dimension and composed primarily (more than 90%) of micropepod nauplii.

Newly hatched *Artemia salina* nauplii, supplemented with wild zooplankton (primarily adult micropepods) were fed to fish larvae from day 12–50 (see also Table 3).

Veligers

Female *Littorina scabra* adult were collected from sea walls surrounding Coconut Island during the low tide preceeding high high tide of the day. At this time, male–female pairs could be located, and the larger of the pair was selected, usually being the female. Females were placed in tubs of filtered sea water where they usually aligned along the water–air interface. In the laboratory females with veligers (3–4 days old) usually spawned throughout the month on the low high or high high tide (± 2 h). A greater percent of females spawned during spring tides. Veligers (maximum dimension approx. 120 μ) were collected and treated as the plankton above and fed to fish larvae.

Food Concentration

Microcopepods were added to rearing containers to a final concentration of 5/ml sea water; veligers to a final concentration of 10–30/ml; *Artemia* to a concentration of 1/ml.

Time Fed

Fish larvae were fed daily from two days after hatching, the time eyes were pigmented and just prior to opening of gut and mouth.

Phytoplankton

Survival of fish larvae was enhanced by addition of phytoplankton cells (local sp. of *Chlorella*) approximately 6–8 μ diameter. Sea water was passed through filters (10 μ) and water containing phytoplankton placed in Fernbach culture flasks (2.8 l) to which 1 ml each of Nutrient A and B (Loosanoff and Davis, 1963) was added. Air was continually bubbled into flasks maintained at 24–25°C under constant light (as above). Dense cultures of *Chlorella* developed in about 2 days and were then added to larval rearing containers at the beginning of experiments. New algal cultures were started every 2 days. Old cultures were not used, as they were frequently toxic. *Chlorella* cells were placed in rearing containers to a final concentration of approximately 1.0×10^4 cells/ml. New *Chlorella* was added when necessary to maintain this concentration. Concentration of algal cells was estimated using a hemocytometer or Coulter counter.

Larval Counts

For most experiments each treatment combination had 3–4 replications and larvae surviving in each replication were counted at the end of the experiment. In other experiments, with smaller volumes of water (*i.e.* 1 l) surviving larvae were counted after the critical day. In still other experiments, smaller numbers of larvae were used and survivors counted daily.

METHODS FOR ANTIBIOTIC AND BACTERIA EXPERIMENTS

Preliminary to testing the effect of antibiotics on survival of larval fish, we tested their effect on bacterial growth in sea water only. Nine-hundred ml of sterilized sea water was placed in each 1-l beaker (Pyrex, straight sides), the antibiotic added and beakers covered with plexiglass covers (hole in center). Salinity and temperature were ambient at 34–36‰ and 23–25°C, respectively. Ambient light at water surface was approximately 430 lux (40 ft-c); oxygen, 6.0–8.0 ppm; pH, 8.0–8.2. A series of six beakers was set up, arranged randomly. Four beakers were inoculated with antibiotic, two were controls with no antibiotic. After 48 h, two of the four treatment beakers were reinoculated with the same concentration of antibiotic to determine the effect of reinoculation on bacterial growth. Bacterial colony counts were taken before addition of antibiotic and every 24 h thereafter for four to five days. Table 6 lists antibiotics tested, together with test concentrations used. Initial concentrations were selected on the basis of recommended base-line dosages for human children. After the effectiveness of the antibiotic on bacterial growth in sea water was determined at this concentration, some were selected for tests with fish eggs and larvae at a wider range of concentrations.

To test effect of antibiotics on larval fish hatching and survival past yolk absorption, larvae were reared as previously described except that volume of sea water and antibiotic type and concentrations were varied. Antibiotics and concentrations tested on larvae are summarized in Table 6. In most tests of the effects of antibiotics on larval hatching and survival, 10 eggs were added to 1-l beakers of sea water, the fish were not fed, and counts of larvae were made daily. These experiments were terminated after all larvae were dead (approx. 5–8 days after hatching, depending on temperature). For several of these experiments bacterial colony counts were also made.

Bacterial colony counts were made on various sea water samples collected from Kaneohe Bay stations, sea water system at Coconut Island and sea water undergoing various treatments such as filtration and ultraviolet radiation.

For counts of bacteria in sea water and culture water containing larval fish, 0.1-ml samples were removed daily with sterile l-ml pipettes for the first 3 days; 0.01-ml samples the remaining days. Other samples (*e.g.* Kaneohe Bay water) were taken with a sterile diposable syringe, capped, and plated into petri plates in 0.5–1.0-ml aliquots. All samples were plated into sterile disposable petri plates containing Difco marine agar (#2216). Plates were incubated at room temperature (24–26°C) for 48 h. The number of bacterial colonies were then estimated using standard microbiological counting procedure.

RESULTS

General Life History and Early Development

C. mate occur in inshore waters of the Hawaiian Islands. They are commonly caught by fishermen in Kaneohe Bay, Oahu, from about March to October. Their distribution during winter months is not definitely known. Breeding continues from late March to late October, with peaks in breeding in May and June. In the laboratory, development from egg to the juvenile stage takes about 48–52 days, by which time the fish have attained a standard length of about 30 mm (Watarai, 1973). Juvenile omaka are most abundant in the fall around floating objects, frequently commensal with jellyfish (Rhizostomata). Sexual maturity in captivity is reached approximately 17–18 months from hatching (24–26°C) at a standard length of about 150 mm. The maximum standard length of adults recorded from Kaneohe Bay is 245 mm.

Table 2 summarizes major developmental stages. Details of the morphology and physiology of development will be given by Miller, Cooney and Santerre (mss. in prep.). Eggs obtained from plankton vary somewhat in size (0.69–0.75 mm in diameter) and developmental stage (6–20 h after fertilization). At 24–25°C eggs hatch approximately 24–25 h after fertilization. Eyes are pigmented by approximately 72 h and mouth and jaws are functional by about 96 h after fertilization. Approximately 3 days after hatching, yolk is about 99% utilized. Larvae are given food on day 2 and feeding is observed by day 3 after hatching. Dry weight decreases as yolk is utilized, followed by an increase after feeding begins approximately 4 days after hatching. If no food is provided most larvae die 6 to 7 days after hatching. The growth rate of larvae to the juvenile stage is described by Watarai (1972).

Effect of Food Type on Survival

Several types of food were tested for their effect on survival of *C. mate* larvae (Table 3). Of those listed, three enabled larvae to survive past the critical period after yolk absorption: microcopepods, veligers and rotifers. Additional experiments testing food types, concentrations and feeding schedules are in progress.

Larvae were fed microcopepods, veligers or mixed microcopepods and veligers for approximately 2 weeks after hatching. After this time larvae were fed *Artemia salina* nauplii supplemented with adult microcopepods.

TABLE 2

Time to selected developmental stages of *Caranx mate*, reared in the laboratory (24–25 °C).

Time* (h-days)	Stage	Approximate mean maximum dimension (mm)
0	Fertilization of egg	0.69–0.75
24–25 h (day 1)	Hatching of larva	2.00
72 h (day 3)	Eyes pigmented	2.40
96 h (day 4)	Gut open, mouth and jaws developed; yolk utilized; feeding begins	2.55
96–144 h (days 4–6)	Critical period; beginning of feeding	2.55
Days 48–52	Juvenile coloration	30
Days 540–550 (18 mos)	Sexual maturity	150

*Hours (days) after fertilization.

C. mate larvae were observed feeding on rotifers (*Brachionus plicatilus*) and survived to day 7 after hatching (40% survival); further experiments with this food type are being performed at the Hawaii Institute of Marine Biology. Larvae did not feed or survive on any other foods listed in Table 3.

TABLE 3

Food types tested on *Caranx mate*, showing feeding response and survival past critical period. Concentration was 5 organisms/ml, except where otherwise indicated.

Food type	Maximum dimension (μ)	Period fed* (days)	Feeding response	Growth–survival (past days 6–7)
Early larval development				
Zooplankton Primarily nauplii of microcopepods *Oithona* and *Paracalanus*	73–150	2–12	+	+
Veligers *Littorina scabra* 10–30/ml	120–130	2–12	+	+
Rotifers *Brachionus plicatilis*	73–150	2–12	+	+
Ciliates *Cyclidium* sp.	20	2–8	?	–
Gymnodinium splendens	50	2–8	–	–
Powdered fish food (Longlife)	100	2–8	–	–
Egg yolk – 1 ml/2 liters (Gerber's)		2–8	–	–
Late larval development				
Artemia salina nauplii	750 × 50	12–50	+	
Zooplankton Primarily adult microcopepods *Oithona* and *Paracalanus*	250–500	12–50	+	

*Number of days after hatching.

Effect of Phytoplankton on Survival

Several experiments revealed higher survival of *C. mate* larvae when local *Chlorella* sp. was added to cultures. The effect of phytoplankton on survival could be due to one or any combination of the following:

(1) Phytoplankton release oxygen, keeping oxygen concentration in cultures at or above saturation.

(2) Phytoplankton remove metabolites which might otherwise reach toxic levels (*e.g.*, ammonia).
(3) Phytoplankton release antibiotic substances, reducing bacterial growth.
(4) Zooplankton survive in cultures longer and provide greater nutrition by feeding on phytoplankton.
(5) *C. mate* larvae obtain some nutrition from phytoplankton.

It would be of interest to perform additional experiments clarifying this point. The *Chlorella* technique and its possible role in larval fish culture were also discussed by Houde at the World Mariculture Society meeting (Houde, 1972).

Effect of Antibiotics on Survival

During early experiments it was found that survival of *C. mate* larvae was increased by treating culture water with antibiotics prior to addition of eggs. Subsequently, experiments were performed attempting to identify bacteria in sea water possibly affecting eggs and larvae, and a number of antibiotics were tested for their effect on density of (1) bacteria in sea water only, (2) bacteria in sea water containing fish larvae, and (3) constituent bacterial genera. Percent hatching and survival of larvae through early development and growth of larvae treated with antibiotics were also recorded. Representative experiments are discussed below.

Interpretation of results must be qualified. Total colony counts may not represent the actual density of bacteria present in the sample. The media used may not be optimal for some species. Methods used are applicable to aerobic bacteria only. Finally, without further experiments to verify pathogenicity, it is not possible to state certainly which species are responsible for mortality. It is possible, however, to correlate bacterial density with percent hatching and survival of larvae; that is, certain antibiotics reduce bacterial density, and those which do also promote hatching success and larval survival.

Identification of Bacterial Genera

Four genera of bacteria were identified from samples originating from a variety of environments. They are *Pseudomonas, Vibrio, Cytophaga* and *Flavobacterium;* all Gram-negative bacteria. Identification was accomplished using the scheme of Shewan *et al.* (1960) and Shewan (1963) for differentiation of Gram-negative bacteria in marine environments. Identification of species was not completed and although two or three forms within each genus were recognized only one species of each genus usually occurred in cultures. Most pseudomonads exhibited green fluorescence, placing them within Group I of genus *Pseudomonas.* Among yellow-pigmented colonies (*Cytophaga* and *Flavobacterium*), *Cytophaga* was predominant; *Flavobacterium* was relatively uncommon. In one experiment the same genera were identified under anaerobic conditions. They thus appear to be facultative anaerobes. Of the four genera, *Vibrio* and *Cytophaga* were more abundant in the anaerobic situation. Sampling was insufficient to state that strictly anaerobic species were absent, and further experimentation is necessary.

Pathogenicity of Bacterial Genera

Although pathogenic species belonging to the above genera in other regions are documented in the literature (*e.g.* Almeida *et al.*, 1968), pathogenicity of the Kaneohe Bay species was not definitely established by satisfaction of Koch's postulates. A species of *Cytophaga* was identified as the probable cause of an eye disease in juvenile and adult *C. mate.* The disease is characterized by marked degeneration of the snout and eyes. The early stage is exemplified by a film-like white covering over the eyes within 24 h from the time infection is first observed. This is followed by rapid necrosis of eye tissue during the next 24–48 h which subsequently spreads to the surrounding tissue. In conjunction with rapid deterioration of the eyes, lesions are formed on the snout, eventually covering the head of the fish. Death usually occurs within 3–5 days. The disease occurs primarily in stressed fish subjected to handling and low oxygen in captivity. It is possible that the same disease may affect survival of larval *C. mate*, but this is yet to be observed or determined.

Abundance of Bacteria

To compare the abundance of bacteria in laboratory cultures with their abundance in Kaneohe Bay, we collected surface sea water samples from different areas in the bay, Coconut Island lagoon, and the sea water system at Coconut Island (Table 4). The mean number of colonies/ml increases from the channel outside of south Kaneohe Bay (Buoys #20 and #8) toward the shores of south Kaneohe Bay (e.g. Kaneohe Marina). Highest, albeit variable, counts of marine bacteria occur in samples taken from the Kaneohe Marine Base sewage outfall, where variability in counts probably reflects changes in outfall with time. The mean number of colonies/ml decreases as water flows through the sea water system at Coconut Island, from Coconut Island Point (the water intake) through various filtration and ultraviolet treatments. The range in mean number of colonies/ml in the bay samples (except Kaneohe Marine base outfall samples) is approximately 80–930 colonies/ml. Table 4 also shows that filtration is relatively effective in reducing bacteria in the sea water.

TABLE 4

Range and mean of bacterial colony counts (total number of colonies/ml) from sea water samples collected at different locations in Kaneohe Bay and the Coconut Island sea water system.

	Channel buoy #20	Channel buoy #8	Coconut Island point	Marine Base sewage outfall	Kaneohe Marina	Coconut Island lagoon
Range	80–360	140–240	200–1020	480–17150	260–930	430–1050
Mean	150	370	580	11070	620	740

Coconut Island sea water system laboratory outflow line

	Outside point (source)	Storage tanks	Single cuno filter	Double cuno filter	Triple cuno filter	Triple cuno filter and ultraviolet
Range	200–1020	320–400	160–400	2–10	0–5	0
Mean	580	360	240	5	2	0

There is seasonal variation in abundance of bacteria. Samples collected in winter months generally contain fewer bacteria. The number of bacteria apparently depends in part on temperature of the sea water, although other factors probably are involved.

In Kaneohe Bay samples, *Pseudomonas* and *Vibrio* species predominate, comprising approximately 40% and 35% of total colonies, respectively. *Cytophaga* species are about 10–20% of the total and *Flavobacterium*, 5–10%.

In laboratory cultures, the density of bacteria was usually significantly higher than in natural waters, as expected. During experiments, total colony counts usually cycled from about 100–1,000,000 colonies/ml. The maximum number of colonies/ml varied from approximately 100,000–1,000,000 colonies/ml. When one compares these values with the normal range of mean colonies/ml in Kaneohe Bay (80–930), it is apparent that the number of colonies/ml may be 10^3-10^5 higher in cultures.

Not only are total colony counts greater in culture situations, but the relative abundance of constituent genera varies. *Pseudomonas* is the most abundant both in the bay and in cultures, but is relatively far more abundant in cultures. While *Vibrio* is more abundant in bay samples than *Cytophaga*, *Cytophaga* is the more abundant of the two in cultures. *Flavobacterium* is even more uncommon in cultures than in the bay.

Effect of Ultraviolet Light on Bacteria

The effect of UV light on bacteria in sea water and resulting larval hatching and survival was tested. Algal and food cultures were also treated with UV in an attempt to reduce their bacterial populations before offering them to larval fish. Table 4 shows that UV light is totally bactericidal when sea water is filtered and then passed through a UV-light unit. To obtain optimal sterilization of sea water, however, precautions must be taken. UV lights should be periodically tested, since they often decline in effectiveness. Sea water should not stand in the UV unit after sterilization, as the bacteria count may greatly increase in a short time. The rate of sea water flow should be adjusted to allow maximal effect. The effectiveness of the UV sterilization unit can be tested periodically by plating out samples from the outflow and making colony counts.

No significant improvement in hatching and survival of *C. mate* larvae resulted from UV sterilization of sea water. In fact, in one experiment, survival was actually significantly poorer in UV-sterilized water. Generally, it appears that unless other deleterious organisms such as fungi are problematic, UV sterilization is unnecessary and possibly undesirable. It is possible that alteration of the normal balance of bacterial genera results in overgrowth of *Pseudomonas* with consequent decreases in larval survival (see also p. 68).

Cultures of phytoplankton, *Artemia* and microcopepods used in feeding larvae often harbor large bacteria populations. The bacteria are significantly reduced by rinsing the algal or food cultures with several changes of

TABLE 5

Effect of ultraviolet light exposure on bacterial counts (total number of colonies/ml) in algal and food cultures*.

Time exposed (min)	Culture	Sample A	Sample B	Mean	Culture growth after exposure
0	*Chlorella*	16000	16000	16000	Yes
1		75	70	72	Yes
3		0	0	0	No
5		0	0	0	No
0	*Artemia*	32000	40000	36000	Yes
1		10000	12000	11000	Yes
3		440	560	500	No
5		300	250	275	No
0	Microcopepods	10000	8500	9250	Yes
1		600	500	550	Yes
3		0	0	0	No
5		0	0	0	No

*900 ml of culture in 1-l glass beakers were exposed. After exposure, 20 ml were removed, diluted to 90 ml and examined for subsequent growth of the organisms.

filtered, sterilized sea water before adding to larval fish cultures. Additional reduction of bacteria is achieved by exposing cultures to 1 min of UV radiation. Results of experiments exposing cultures to UV light (Table 5) show that a 1-min exposure is sufficient to significantly reduce bacteria and 3 min or more is totally bactericidal, except for *Artemia salina* cultures. Exposure of *Artemia* for 3 min effectively reduces, but does not completely eleminate bacteria. None of the organisms tested was able to withstand exposure longer than 1 min. This technique for reducing bacterial contamination in food and algal cultures must be used cautiously to be sure organisms can withstand a 1-min exposure; some species may not survive such treatment.

Growth of Bacteria in Sea Water only

Bacterial colonies were counted from samples removed from sea water controls (see **Methods**). No algae, larvae or antibiotics were added. Fig. 1 shows the increase in density of bacteria for the experimental period. An

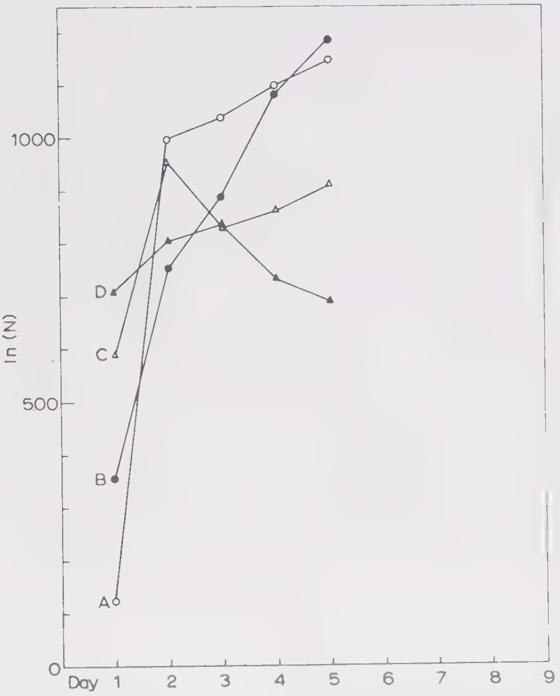

Fig. 1. Change in density of bacteria (all genera combined) in control cultures of sea water only. Y = Mean ln (N), where N = Total number of bacterial colonies/ml (3 replicates); X = Day of experiment. A-Experimental control with low initial number of colonies/ml; B and C-Experimental controls with intermediate initial number of colonies/ml; D-Experimental controls with high initial number of colonies/ml.

interesting feature of bacterial growth in these sea water cultures is that the initial density of bacteria appears to affect subsequent bacterial growth rate. In sea water with lower initial bacterial densities, bacteria rapidly increase to a high density (Fig. 2 A and B). In sea water with higher initial bacterial densities (Fig. 1 C and D) bacteria increase less rapidly, often stabilizing at a lower density than in cultures with lower initial densities. The rapid increase to a high density (in terms of total colonies/ml) probably represents an overgrowth of *Pseudomonas* species, which appear to have a higher growth rate in culture than *Cytophaga* and *Vibrio*. This is discussed further below.

Growth of Bacteria in Sea Water with Fish Larvae

Other experiments, similar to above except for the addition of 10 *C. mate* eggs to each 1-l beaker, show results comparable to those above. The increase in density of bacteria over time is shown in Fig. 2. Again, lower initial densities result in faster bacterial growth. In the experiment

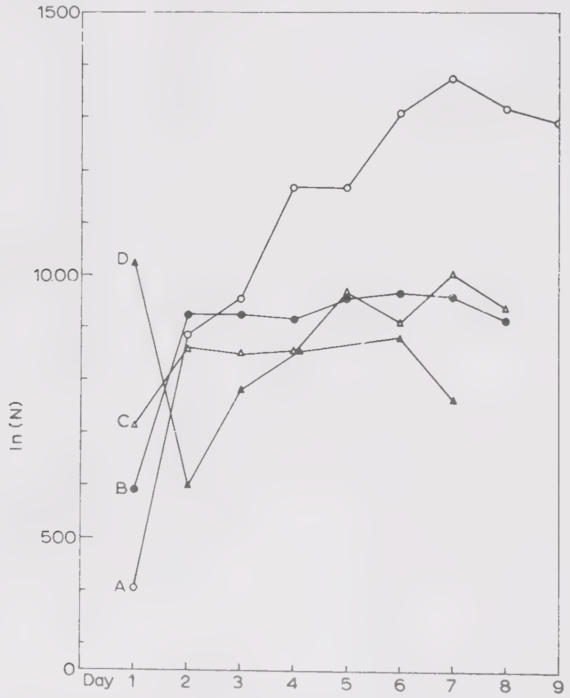

Fig. 2. Change in density of bacteria (all genera combined) in control cultures with *C. mate* larvae. Y = Mean ln (N), where N = Total number of bacterial colonies/ml (3 replicates); X = Day of experiment (= day after fertilization of eggs). A-Experimental controls with low initial number of colonies/ml; B and C-Experimental controls with intermediate initial number of colonies/ml; D-Experimental controls with very high initial number of colonies/ml (high count probably due to leaving sea water in ultraviolet light unit after sterilization; UV light off).

depicted in Fig. 2 D a very high initial bacterial count existed. This resulted from allowing sea water to stand in the UV unit after sterilization with UV light off for some time before sampling. Consequently, *Pseudomonas* increased rapidly, overgrowing *Cytophaga* and *Vibrio*. Percent hatching of eggs was low in this situation; poor hatches generally occurred when the initial total bacterial colony counts exceeded a density of approximately 22 000 colonies/ml (ln 22 000 colonies/ml = 10.000 approx.) on day 1.

An example of relative density of bacterial genera in larval control cultures not treated with antibiotics is given in Fig. 3, where larval survival is also indicated. *Pseudomonas* is most abundant in all these cultures, including the experiment represented, followed in abundance by *Cytophaga* and lastly by *Vibrio*. *Flavobacterium* was not observed, and was generally rare in laboratory cultures. Considerable mortality occurred in the first 2 days due to reduced hatching. In the typical example of Fig. 3, bacterial density remained relatively stable and mortality was about average for controls (no antibiotic treatment). In other experiments with higher or lower initial bacterial densities, bacterial density tended to fluctuate greatly and mortality was higher.

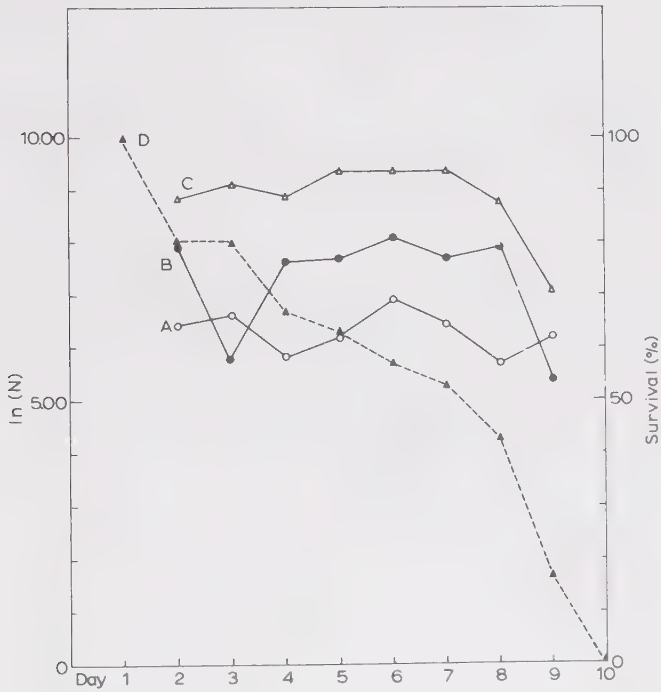

Fig. 3. Change in density of constituent bacterial genera in control cultures of *C. mate* larvae and percent survival of *C. mate* larvae. Left Y-axis = Mean number of colonies/ml (3 replicates); Right Y-axis = Mean percent survival of larvae; X = Day of experiment. A-*Vibrio*; B-*Cytophaga*; C-*Pseudomonas*; D-Mean percent survival of *C. mate* larvae (dashed line).

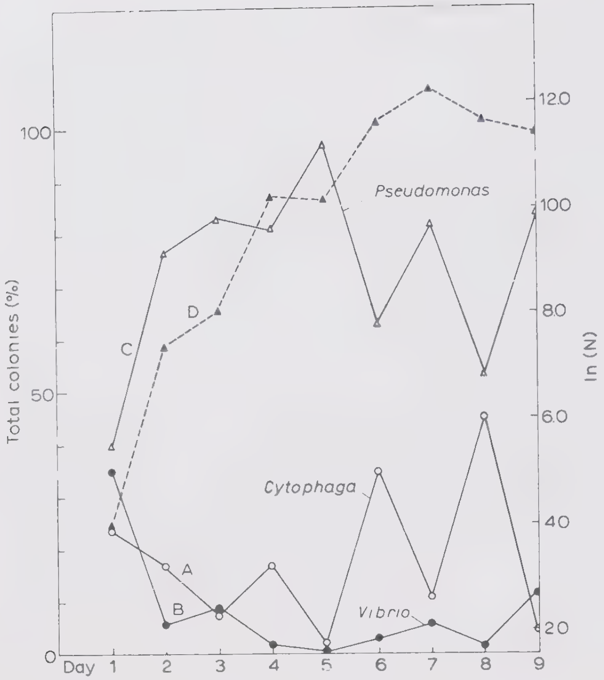

Fig. 4. Cycling density of bacterial genera in terms of percent of total bacterial colonies/ml (solid lines). Total number of bacterial colonies (all genera combined) is indicated by broken line. Left Y axis = Mean percent of total bacterial colonies/ml; Right Y axis = ln (N), where N = Mean number of total bacterial colonies. X = Day of experiment. A-*Cytophaga*; B-*Vibrio*; C-*Pseudomonas*; D-Total.

When counts for all control cultures were combined, *Pseudomonas* colonies comprised an average of 74% of the total colonies; *Cytophaga*, 18%, and *Vibrio*, 6%. In Fig. 4, an example is given of relative density of genera in terms of percent of the total number of colonies/ml per day. The pattern exhibited is the one most frequently observed in cultures, with a daily cycle in abundance of *Pseudomonas* and *Cytophaga*. Initially, all three genera are nearly equivalent in density. As *Pseudomonas* density increases from day 1–2 (Fig. 4 C), *Cytophaga* density decreases (Fig. 4 A). Thereafter, each increase in density of one genus correlates with a decrease in the other. *Vibrio* density in general does not exhibit as definitive a cycle (Fig. 4 B), but tends to interact with density of *Pseudomonas* on certain days. Sea water, prior to use in a culture situation, usually contains the three major genera in approximately equivalent abundance. In culture, the negative correlation of density of *Pseudomonas* with density of *Cytophaga* and perhaps *Vibrio*, suggests that a competitive interaction exists, characterized by cycling abundance of bacterial genera. Finally, after a number of days (depending mostly upon volume of water)

TABLE 6

Antibiotics tested for effect on bacterial growth in sea water and on survival of *Caranx mate* larvae. Antibiotics effective in increasing hatch and survival of larval fish are indicated by asterisk. Antibiotics found toxic to larval fish are indicated by cross (toxic at all conc. tested). (With the exception of some tetracyclines, these antibiotics have not been FDA approved for aquaculture of fish.)

Microbial Derivatives of Eubacteriales

Name of antibiotic	*Aerosporin (Polymyxin B sulfate)	*Coly-Mycin (Polymyxin E, Colistin sulfate)
Derivation	*Bacillus polymyxa*	*Aerobacillus colistinus*
Tested	Sea water and larvae	Sea water and larvae
Concentrations tested (ppm)		
Bacteria in sea water	1, 10, 20, 25, 30, 40, 50, 60 70, 75, 80, 90, 100	80
Larvae	1, 8, 10, 16, 20, 25, 30, 40, 50, 60, 70, 75, 80, 90, 100	1, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100
Effect on bacteria in sea water	Suppression of *Cytophaga* spp. No suppression of *Vibrio* spp. beyond day 4. No suppression of *Pseudomonas* spp.	Significant suppression of all bacteria for at least 5 days
Recommended concentration for larvae (ppm)	10–30	10–40
Toxic effects (mortality and/or retarded development)	Over approx. 40 ppm	Over approx. 40 ppm

Comments: Both of these antibiotics are effective in increasing hatch and survival. Together with Ilotycin (erythromycin gluceptate) and Penicillin G, these antibiotics are the most effective tested.

Microbal Derivatives of Actinomycetales

Name of antibiotic	† Chloromycetin (Chloramphenicol)	Garamycin (Gentamicin sulfate)
Derivation	*Streptomyces venezuelae*	*Micromonospora* sp.
Tested	Sea water and larvae	Sea water only
Concentration tested (ppm)		
Bacteria in sea water	50	3
Larvae	25, 50	Not tested
Effect on bacteria in sea water	Some suppression of bacteria	*No* significant suppression of bacteria

TABLE 6 (continued)

Recommended concentration for larvae (ppm)	Not recommended 25 and 50 both toxic	Not tested
Toxic effects	Toxic at 25 and 50	Not tested

Comments: Chloromycetin may be less toxic at lower concentrations and Garamycin more effective at higher concentrations. A wider range should be tested.

Name of antibiotic	*Ilotycin (Erythromycin gluceptate)	Kantrex (Kanamycin sulfate)
Derivation	*Streptomyces erythreus*	*Streptomyces kanamyceticus*
Tested	Sea water and larvae	Sea water only
Concentration tested (ppm)		
Bacteria in sea water	4, 8, 11, 12, 16	15
Larvae	1, 4, 8, 12, 16	Not tested
Effect on bacteria in sea water	Significant suppression of total bacteria count for 6 days at all non-toxic concentrations. All bacteria genera suppressed	No significant suppression
Recommended concentration for larvae (ppm)	10–12	Not tested
Toxic effects	Over approx. 12 ppm	Not tested

Comments: Kantrex concentration of 15 ppm tested on sea water may be too low to affect bacteria colony count. More tests should be made. This antibiotic not tested on larvae.

Name of antibiotic	Streptomycin (Streptomycin sulfate)	Neomycin (Neomycin sulfate)
Derivation	*Streptomyces griseus* and other *Streptomyces* spp.	*Streptomyces fradiae*
Tested	Sea water and larvae	Sea water only
Concentrations tested (ppm)		
Bacteria in sea water	50	200
Larvae	50, 100	Not tested

TABLE 6 (continued)

Effect on bacteria	Some suppression of bacteria for 1 day, then same as control	Only slight suppression of bacteria
Recommended concentration for larvae (ppm)	50 – but streptomycin not very effective in reducing mortality	Not tested
Toxic effects	Toxic at 100	Not tested

Comments: A wider range of Streptomycin should be tested, but indications are that it is relatively ineffective.

Name of antibiotic	† Tetrex (Tetracycline HCl)	† Vibramycin (Doxycycline)
Derivation	Various *Streptomyces* spp.	Synthetic tetracycline
Tested	Sea water and larvae	Sea water and larvae
Concentrations tested (ppm)		
Bacteria in sea water	200	5, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100
Larvae	50	Same as sea water
Effect on bacteria in sea water	Significant suppression for 1 day, then same as control	Slight suppression for 5 days
Recommended concentration for larvae (ppm)	Toxic at 50	Toxic at all concentrations
Toxic effects	Toxic at 50	Toxic at all concentrations

Comments: Tetrex and Vibramycin probably toxic at all concentrations.

Microbial Derivatives of Fungi

Name of antibiotic	*Geopen (Disodium carbenicillin)	*Penicillin G (Potassium penicillin G)
Derivation	Semi-synthetic penicillin	*Penicillum notatum* and other *Penicillum* spp.
Tested	Sea water and larvae	Sea water and larvae
Concentrations tested (ppm)		
Bacteria in sea water	100	50
Larvae	10, 50, 100	10, 25, 50, 75, 100

TABLE 6 (continued)

Effects on bacteria in sea water	Significant suppression of bacteria for 5 days then equal to control	Significant suppression for 2–3 days then equal to control
Recommended concentration for larvae (ppm)	10–50	50
Toxic effects	Over approx. 50 ppm	Over approx. 60 ppm

Comments: These two penicillin derivatives, together with Polycillin N, significantly increase hatching and survival through critical period. However, they characteristically decrease bacteria count for only a short period (depending on concentration), thereafter allowing rapid increase to control count level.

Name of antibiotic	*Polycillin N (Ampicillin trihydrate)	*Keflin (Sodium cephalothin)
Derivation	Semi-synthetic penicillin with extended action against gram-negative rods	*Cephalosporium* sp.
Tested	Sea water and larvae	Larvae only
Concentrations tested (ppm)		
Bacteria in sea water	25, 50, 75, 100	Not tested
Larvae	10, 25, 50, 75, 100	50, 100
Effect on bacteria in sea water	Significant suppression 3–4 days then equal to control	Not tested
Recommended concentration for larvae (ppm)	10–25	50
Toxic effects	Over approx. 50 ppm	Toxic at 100

Comments: Further experiments should be made comparing the effectivity of Geopen, Penicillin G, and Polycillin in reducing bacterial counts and increasing hatch and survival. Presently they appear to be equally effective. Keflin at 50 ppm significantly improved hatching and survival of larvae, but an insufficient concentration range has been tested to determine the optimal range and toxity level.

Chemical Anti-microbial Agents

Name of antibiotic	Furadantin (Nitrofurantoin)	Sulfadiazine (*N*′-2-pyrimidinylsutaniamide)
Derivation	1-[(5-Nitrofurfurylidene)-amino] hydantoin	As above

TABLE 6 (continued)

Tested	Sea water and larvae	Sea water only
Concentrations tested (ppm)		
Bacteria in sea water	7	150
Larvae	50, 100	Not tested
Effect on bacteria in sea water	No significant suppression of bacteria	Actually enhanced bacterial growth (approx. 10^5 times greater than control level)
Recommended concentration for larvae (ppm)	50	Not recommended
Toxic effects	Toxic at 100	Not tested

Comments: Furadantin not as effective in increasing hatching and survival as other suitable antibiotics. However, a wider range should be tested.

densities return to levels approximately the same as they were initially. Further, when the three genera are nearly equivalent in abundance, the total number of bacterial colonies is less. In the light of these results it seems best to limit initial treatment of water to single Cuno filtration so that the abundance of genera is approximately equivalent in the beginning of the experiment and overgrowth of *Pseudomonas* does not occur.

Effect of Antibiotics on Bacteria in Sea Water only

A number of antibiotics were first tested for their effect in decreasing bacteria in sea water. The antibiotics tested, derivation, concentrations and effect on bacteria are summarized in Table 6. Antibiotics tested were selected for a variety of reasons. Some were previously shown to be effective in increasing hatching or larval survival in fishes (*e.g.* Oppenheimer, 1955), others were selected because of comparable derivation or structure. Some were selected because of their effect on human gram-negative bacteria. Of the antibiotics tested, those found effective in decreasing bacteria in sea water cultures were: Aerosporin (polymyxin B sulfate), Coly-Mycin (polymyxin E), Ilotycin (erythromycin gluceptate), Geopen (disodium carbenicillin), Penicillin G, and Polycillin N (ampicillin trihydrate). Sulfadiazine actually enhances bacterial growth, resulting in densities of bacteria approximately 10^5 times greater than controls. Those antibiotics found most effective in reducing bacterial density in sea water were selected for testing at a greater range of concentrations.

Effect of Antibiotics on Hatching and Survival of Larvae

Several antibiotics were tested which significantly increased larval hatching and survival. Of these, the penicillins, polymyxins and erythromycin were the most effective. Some other antibiotics in Table 6 may be effective in reducing bacteria but are toxic to larvae (*e.g.* tetracyclines), and some require further testing at wider ranges of concentrations (*e.g.* keflin). Streptomycin, an antibiotic frequently used in rearing marine larvae (*e.g.* Shelbourne, 1964) only slightly reduced bacteria, and no significant improvement in survival was apparent. The most effective antibiotics are summarized in Table 7 in order of increasing effectiveness in promoting hatching and larval survival. In Table 8 they are classified into groups according to chemical mode of action. Examples selected from these major groups of antibiotics are discussed below [Aerosporin (polymyxin B), Polycillin N (ampicillin), and Ilotycin (erythromycin)] to illustrate the effect of antibiotics on bacterial density and larval survival.

TABLE 7

Mean percent hatching and survival (of original eggs stocked) past critical period of *C. mate* given different antibiotic treatments. Antibiotics arranged approximately in order of increasing effectiveness. One treatment on day 1 only. Data shown are means of all experiments on the particular antibiotic shown. Number of replicates at least 5, usually more; all percent hatches of larvae given antibiotic treatments shown were significantly different from controls ($P < 0.01$) except for Streptomycin.

Treatment	Antibiotic concentration (ppm)	Mean percent hatching	Mean percent survival (past days 6–7)
Controls (no antibiotic)	–	67	36
Streptomycin	50	66	42
Keflin	50	74	67
Polycillin N	10–25	90	55
Penicillin G	50	85	75
Geopen	10–50	85	77
Aerosporin (Polymyxin B)	10–30	87	85
Coly-Mycin (Polymyxin E)	10–40	94	87
Ilotycin (Erythromycin)	10–12	94	93

TABLE 8

Group, chemical nature and mode of action of some antibiotics tested. Antibiotics effective in increasing percent hatch and survival of *Caranx mate* designated with asterisk. [Information modified from Evans (1965), Gale (1966), Vol. 16 of the 16th Symposium of General Microbiology (1966), Gottlieb and Shaw (1967), and Garrod and O'Grady (1968) 1].

Group and chemical nature	Nonproprietary name (with proprietary examples)	Empirical formula	Mode of action §
Polypeptides (cyclic polyamides)	Polymyxin B (*Aerosporin)	$C_{56}H_{98}N_{16}O_{13}$	1
	Polymyxin E= Colistin A (*Coly-Mycin)	$C_{53}H_{100}N_{16}O_{13}$	
Penicillins and cephalosporins (water-soluble acids, α-amino-β-lactams fused to sulfur-containing ring)	Benzylpenicillins (*Penicillin G)	$C_{16}H_{18}N_2O_4S$	2
	(*Geopen)		
	Ampicillin (*Polycillin N)	$C_{16}H_{19}N_3O_4S$	
	Cephalothin (*Keflin)	$C_{16}H_{16}N_2O_6S_2$	
Aminoglycosides (water-soluble bases containing amino sugars)	Streptomycin	$C_{21}H_{39}N_7O_{12}$	3
Macrolides (large ring lactones with at least 1 sugar moiety)	Erythromycin (*Ilotycin)	$C_{37}H_{67}NO_{13}$	4
Tetracylines (amphoteric, highly substituted naphthacene derivatives)	Tetracyline (Tetrex)	$C_{22}H_{24}N_2O_8$	4
	Oxytetracyline (Vibramycin)	$C_{22}H_{24}N_2O_8$	
Miscellaneous (*p*-nitrophenylserinol derivative)	Chloramphenicol (Chloromycetin)	$C_{11}H_{12}Cl_2N_2O_5$	4

§ Classification of general modes of action:

Group 1: Affect permeability of bacterial cell membrane causing leakage of substances of small molecular weight. Only antibiotics that kill both resting stages and growing bacteria. Bactericidal and bacteriostatic; rapidly induce cessation of bacterial respiration (especially Colistin).

TABLE 8 (continued)

Group 2: Prevent synthesis of cell wall during bacterial growth so cell lysis occurs (membrane ruptures). Require bacterial growth to act. Bactericidal; long period of contact with bacteria necessary.

Group 3: Inhibition of protein synthesis. Require bacterial growth to act. Bacteriostatic; period of contact with bacteria necessary.

Group 4: Inhibition of protein synthesis. Require bacterial growth to act. Bacteriostatic; but inhibit protein systhesis and growth immediately when bacteria exposed.

Groups 2 and 3 are synergistic. Groups 1 and 4 are sequentially synergistic. Groups 1 and 4 are often antagonistic to groups 2 and 3.

Aerosporin (polymyxin B sulfate) is a polypeptide derived from *Bacillus polymyxa.* Fig. 5 shows the effect of different concentrations of Polymyxin B on density of *Pseudomonas, Cytophaga* and *Vibrio* over the experimental period.

Concentrations of 25, 50, 75 and 100 ppm were tested, but only the effects of 25 and 50 ppm are shown in the figure. Concentrations over 50 ppm are toxic to the fish larvae. Polymyxin B appears to suppress *Cytophaga* most significantly; there was less suppression of *Vibrio* and apparently no suppression of *Pseudomonas* species (Fig. 5). The density of *Pseudomonas* at 25 and 50 ppm is actually higher than the density in controls. The suppression of *Cytophaga* and *Vibrio* apparently results in an overgrowth of *Pseudomonas* species.

Nevertheless, treatment of cultures with 25 and 50 ppm significantly increases hatching survival of *C. mate* larvae (Fig. 6). A concentration of 50 ppm, although resulting in better hatching and survival than controls, may be slightly toxic, retarding development to some degree. Other experiments show that lower concentrations of Polymyxin B (approx. 10–20 ppm) are most effective in increasing hatching and survival, without retarding development (Fig. 7); the slightly higher temperature of Fig. 7 was judged not to have affected the antibiotic results, although yolk absorption and subsequent mortality was earlier.

An increase in percent hatching and survival results from treating larval cultures with Polymyxin B although *Pseudomonas* species are not affected by this antibiotic. This may indicate that *Cytophaga* and/or *Vibrio* are decreasing hatching and larval survival more significantly. Further experimentation is necessary to verify this.

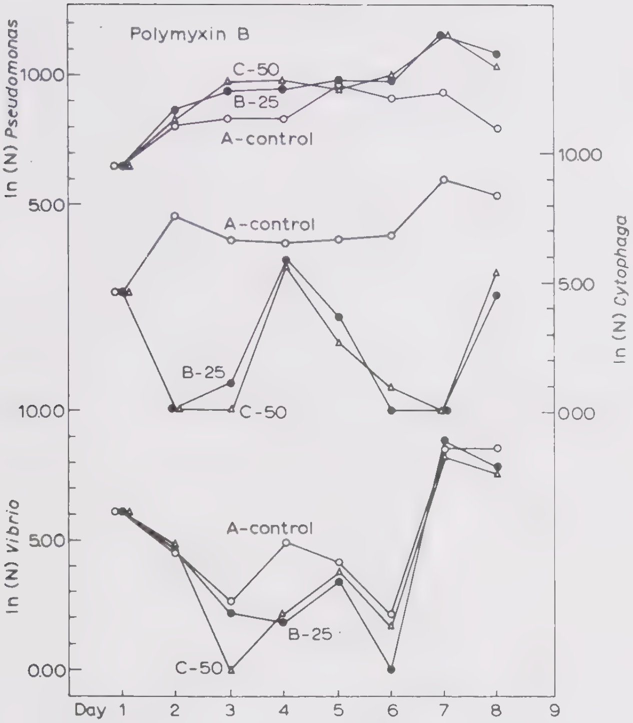

Fig. 5. Changes in densities of *Pseudomonas, Cytophaga*, and *Vibrio* in *C. mate* larval cultures treated with Polymyxin B. Y = Mean ln (N), where N = Number of colonies/ml (3 replicates); X = Day of experiment. A-Control, no antibiotics; B-25 ppm Polymyxin B; C-50 ppm Polymyxin B.

Ilotycin (erythromycin gluceptate) is a macrolide (see Table 8) derived from *Streptomyces erythreus*. Fig. 8 shows the effect of various concentrations of this antibiotic on *Pseudomonas* density. *Cytophaga* and *Vibrio* were suppressed in a similar manner. The high counts observed in this experiment may be due to low initial density; in other comparable experiments with erythromycin far lower counts were observed. Concentrations of 4, 8, 12 and 16 ppm were tested and 16 ppm was found to retard development of larvae.

In spite of the high bacterial densities in this experiment after day 1, Fig. 9 shows that hatching and survival of larvae is significantly improved at 4–12 ppm, perhaps because all genera are suppressed instead of only one or two as with other antibiotics. The optimal concentration (determined from three comparable experiments) is 12 ppm. Erythromycin was generally the most effective antibiotic in increasing both hatching and survival of larvae past the critical stage.

Polycillin N (ampicillin trihydrate) is a semi-synthetic penicillin derivative, a water-soluble acid. Polycillin N is most effective in reducing density

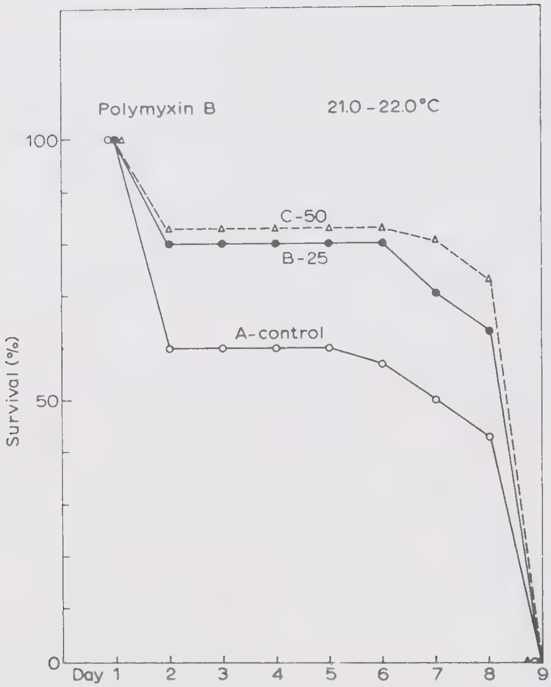

Fig. 6. Percent survival of *C. mate* larvae (not fed) in cultures treated with Polymyxin B (same experiment as Fig. 5) at 21–22 °C. Y-axis = Mean percent survival of larvae (3 replicates); X-axis = Day of experiment. A-Control, no antibiotics; B-25 ppm Polymyxin B; C-50 ppm Polymyxin B. Dashed line indicates survival at a concentration of Polymyxin B which slowed development and may be considered toxic.

of *Cytophaga* (Fig. 10); *Pseudomonas* and *Vibrio* are also suppressed but to a lesser extent. Although concentrations of 25, 50, 75 and 100 ppm were tested, only the results at 25 and 50 ppm are shown; higher concentrations were toxic to larvae. Further, although 50 ppm was effective in reducing bacteria, it appeared to delay larval development slightly. Other experiments indicate that a lower range of approximately 10–25 ppm Polycillin N is maximally effective in increasing hatching and survival of larvae.

Fig. 11 shows the effect of 25 and 50 ppm Polycillin N on the hatching and survival of larvae. Though a significant difference from the control was determined, it can also be seen that erythromycin and polymyxin B (Figs. 7, 9) resulted in better larval survival. Results of other experiments testing penicillin dirivatives showed similar results to those with Polycillin.

Growth of Larvae treated with Antibiotics

Comparisons of growth and development of larvae treated with Polymyxin B, Streptomycin, Erythromycin and Penicillin G with growth of

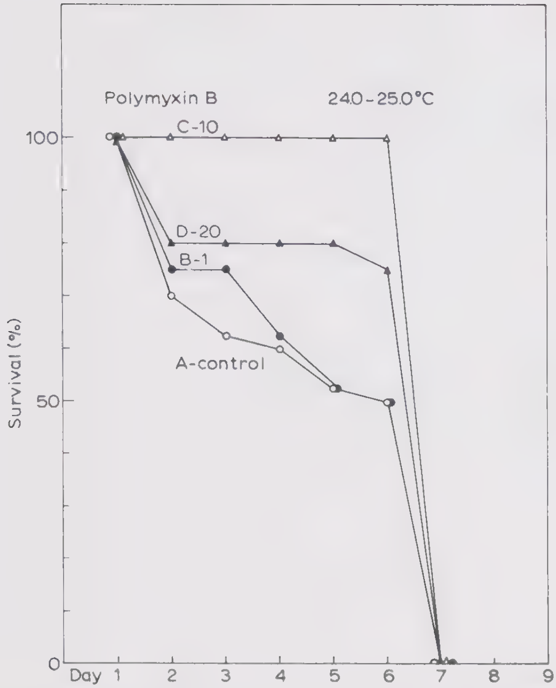

Fig. 7. Percent survival of *C. mate* larvae (not fed) in cultures treated with Polymyxin at 24–25°C. Y = Mean percent survival of larvae (5 replicates); X = Day of experiment. A-Control, no antibiotics; B-1 ppm Polymyxin B; C-10 ppm Polymyxin B; D-20 ppm Polymyxin B.

untreated larvae were made. No significant difference in growth rate was observed at optimal concentrations of these antibiotics. Above these concentrations (see Table 6) retardation in development and growth was often observed.

Number of Antibiotic Treatments

In several experiments, repeated application of an antibiotic was tested on both bacterial density and larval hatching and survival. In most experiments, a treatment was given on days 1 and 3. For most antibiotics, no significant difference in bacterial density or larval survival was noted between those treated on day 1 only and those treated on both days 1 and 3. In a few cases a slightly greater reduction of bacteria occurred with two treatments, but bacterial density usually increased to control levels within a day.

Generally, bacterial populations decreased for the first few days after initial treatment on day 1. The subsequent rate of increase was greatest when initial density was lowest. After a few days bacterial density usually equalled or surpassed the control level: apparently the bacteria developed some resistance to the antibiotic by this time. A second application of the

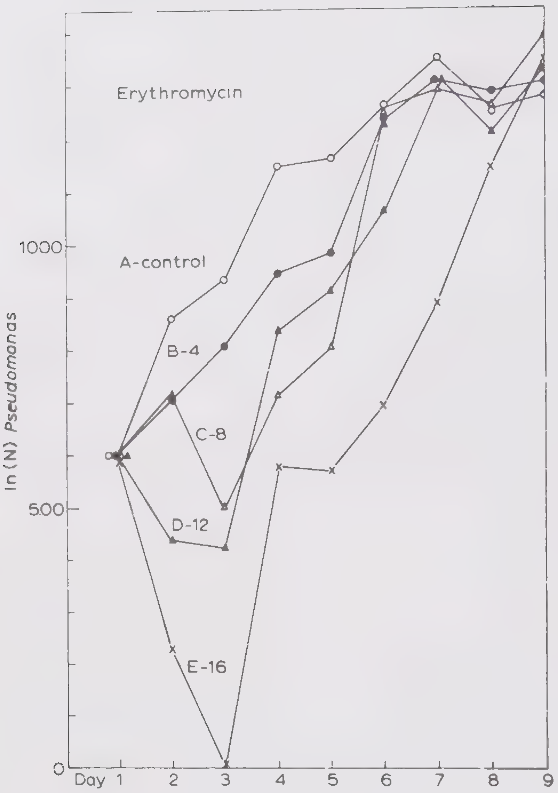

Fig. 8. Change in density of *Pseudomonas* in *C. mate* larval cultures treated with Erythromycin. Y = Mean ln (N), where N = Number of *Pseudomonas* colonies/ml (3 replicates); X = Day of experiment. A-Control, no antibiotics; B-4 ppm Erythromycin; C-8 ppm Erythromycin; D-12 ppm Erythromycin; E-16 ppm Erythromycin.

same antibiotic, therefore, usually had little effect, at least on day 3. Addition of antibiotic again on a later day may prove more effective.

CONCLUSIONS AND DISCUSSION

The major aerobic genera of marine bacteria present in Kaneohe Bay and in laboratory larval fish cultures have been identified. Considerable work remains in identification of species and determination of their relative abundance in different culture situations. Experiments verifying species responsible for *C. mate* larval mortality should be continued. Results so far indicate that a species of *Cytophaga* may be an important pathogen, reducing hatching and survival of larvae. This genus is more abundant in cultures than in the open bay. A species of *Cytophaga* is probably responsible for a degenerative eye disease in juvenile and adult *C.*

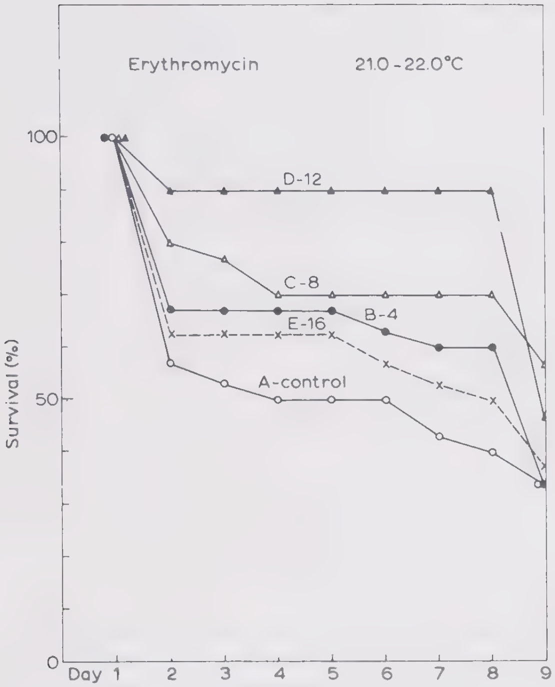

Fig. 9. Percent survival of *C. mate* larvae (not fed) in cultures treated with Erythromycin (same experiment as Fig. 8) at 21–22°C. Y = Mean percent survival of larvae (3 replicates); X = Day of experiment. A-Control, no antibiotics; B-4 ppm Erythromycin; C-8 ppm Erythromycin; D-12 ppm Erythromycin; E-16 ppm Erythromycin. A concentration of 16 ppm (dashed line) was toxic to larvae.

mate. Further, two of the most effective antibiotic groups significantly suppress *Cytophaga* growth in cultures (polymyxins and penicillins), having less effect on *Pseudomonas* and *Vibrio*. The observation, however, that erythromycin (which suppresses all 3 genera) is the most effective of all antibiotics tested suggests that the other genera may contain pathogenic species. Also, high initial colony counts of *Pseudomonas* species are often associated with poor hatches.

The three groups of antibiotics appearing most effective in increasing survival are the polymyxins, penicillins and erythromycin. Most effective is erythromycin. An inexpensive form of erythromycin is available in tablet form, called Maracyn (Mardel Laboratories). The effectiveness of this form is presently being compared against Ilotycin (Eli Lilly & Co.).

The antibiotic streptomycin sulfate has been used frequently in larval culture work (e.g. Loosanoff and Davis, 1963; Shelbourne, 1964). Surprisingly, we found this antibiotic relatively ineffective in reducing bacteria or increasing hatching and survival (Table 7). The reasons for this are

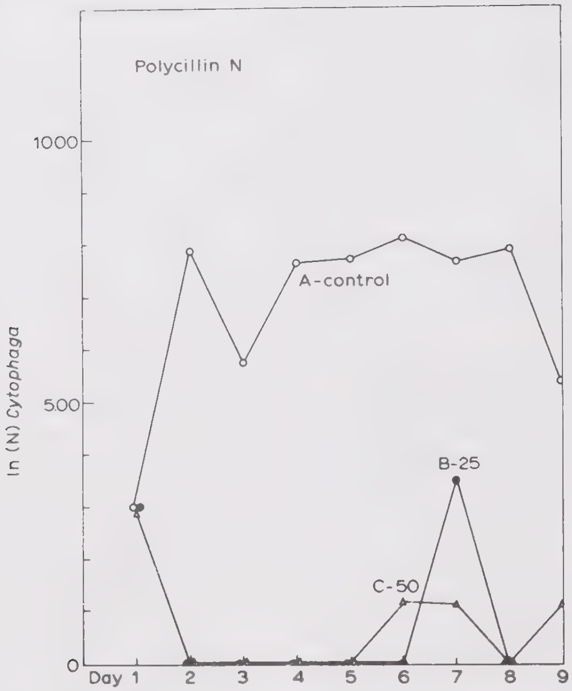

Fig. 10. Change in density of *Cytophaga* in *C. mate* larval cultures treated with Polycillin N. Y = Mean ln (N), where N = Number of *Cytophaga* colonies/ml (3 replicates); X = Day of experiment. A-Control, no antibiotics; B-25 ppm Polycillin N; C-50 ppm Polycillin N.

unclear. Hawaiian species of bacteria may be resistant to streptomycin, or some factor in our culture environment may inhibit the action of streptomycin.

The group 1 antibiotics, or polymyxins, are the only antibiotics which act on bacteria both in resting and growing stages (Table 8). Polymyxins are surface active agents, disrupting the cell membrane; they are bactericidal and bacteriostatic. Group 2 antibiotics, or penicillins, are also bactericidal, but require a longer period of contact with bacterial cells to be effective. They act by inhibiting synthesis of the bacterial cell membrane so that cells eventually lyse. The penicillins require growth of bacteria to be effective. Group 3, or streptomycin, acts on bacteria by inhibiting protein synthesis, altering the conformation of ribosomal RNA. Streptomycin also requires growth at the time of application for effect. This antibiotic is bacteriostatic, bacterial cells continuing to respire after application of the antibiotic although not growing. Group 4 includes several chemical sub-groups: erythromycin, tetracyclines, and chloramphenicol. These antibiotics also inhibit protein synthesis, but unlike streptomycin they act on bacteria almost immediately upon contact. Group 4 antibiotics are also bacteriostatic.

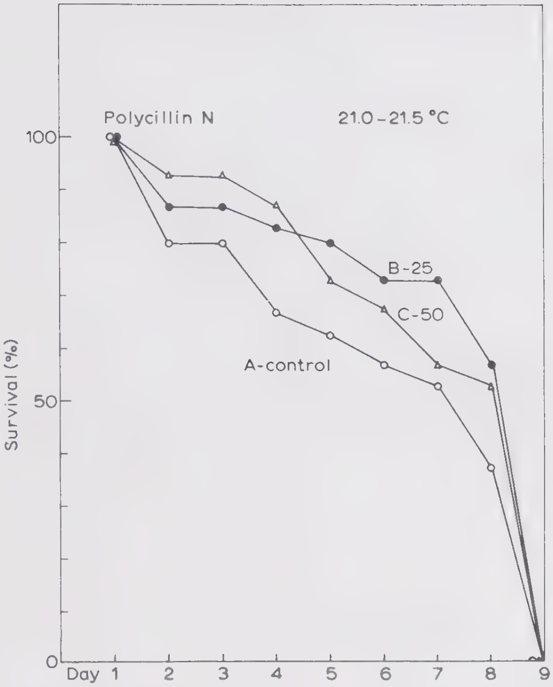

Fig. 11. Percent survival of *C. mate* larvae (not fed) in cultures treated with Polycillin N (same experiment as Fig. 10) at 21–21.5°C. Y = Mean percent survival of larvae (3 replicates); X = Day of experiment. A-Control, no antibiotics; B-25 ppm Polycillin N; C-50 ppm Polycillin N.

It is important to understand the mechanisms by which antibiotics affect bacteria in order to determine which groups are synergistic and can be used in conjunction with one another and which are antagonistic and inhibit the effect of one another. Groups 2 and 3, the penicillins and streptomycin, are synergistic. Both require growth of bacterial cells for effectiveness. Groups 1 and 4 may also be synergistic if used in sequence. Groups which kill bacterial cells on contact (polymyxins) or stop bacterial growth immediately (group 4, e.g. erythromycin) are antagonistic in action to those which require a period of contact with growing bacteria, such as the penicillins and streptomycin.

The application of antibiotics in different sequences might achieve maximum control of bacteria over extended periods, for example, an initial treatment of erythromycin followed by a treatment of polymyxin on about day 5 when bacterial growth again increases. Sequential treatments may solve the problem of bacterial overgrowth of species of a more resistant genus (*i.e. Pseudomonas*) when another genus is suppressed (*i.e. Cytophaga*), such as occurs when cultures are treated with Polymyxin B

(Fig. 5). The combination or sequential use of different antibiotics should have a wider spectrum of effect. Such treatments may also overcome the tendency for bacterial species to become resistant when they are selected by antibiotic application. The rapid rise of *Pseudomonas* at 16 ppm of erythromycin on day 4 (Fig. 8) may be a case in point.

Most antibiotics currently used in the control of marine bacteria in larval cultures were developed for treatment of mammalian diseases, particularly in man, where repeated application at short time intervals is a standard practice. Such antibiotics may not be the most effective in a marine environment. Research on naturally-occurring antibiotics in the sea (*e.g.* produced by marine algae) may reveal more effective antibiotics for control of marine bacteria in laboratory cultures of larvae which may then also require repeated rather than single applications.

In this report techniques were delineated for rearing marine carangid larvae (primarily *C. mate*) in the laboratory. The extension of laboratory results from small volumes of water (closed systems) to mass rearing techniques (open systems) will require modification of present techniques. For example, if larger volumes of continuously flowing sea water are used, application of antibiotics may be complicated and expensive. In this event hatching may be improved by treating eggs with antibiotics before placing them in a mass culture system. Additional antibiotic treatment may be unnecessary if balanced bacterial populations are maintained, as expected in continuously flowing sea water. The provision of food to large numbers of larvae in greater volumes of sea water can be difficult (May, 1970). In Hawaii, where microcopepods and veliger larvae are readily available all year, this problem is not so acute. A rearing system could be designed to automatically pump and sort appropriate wild plankton to feed fish larvae. A method of collecting large quantities of plankton by pumping was used by G.O. Schumann in mass culture of *Scomber japonicus* (described in Bardach, 1968). The design of a mass culture system for carangid larvae should also include means of controlling temperature, salinity, pH, metabolites and light. If a suitable mass rearing system can be designed and maintained economically, it should be possible to cultivate *C. mate* on a commercial scale.

One final obstacle to carangid aquaculture remains. Presently, we are dependent for material upon collection of planktonic eggs from approximately March to October. Future aquaculture of *C. mate* is ultimately dependent upon delineation of techniques for inducing matuaration and spawning of carangids in captivity.

ACKNOWLEDGEMENTS

We appreciate the advice and council of Dr. Philip Helfrich, Hawaii Institute of Marine Biology. June Lum, Leigh Maginniss and Lloyd Watarai, Hawaii Institute of Marine Biology, provided considerable assistance in various aspects of the larval rearing. Also, Lester Zukeran and staff, Hawaii Institute of Marine Biology, contributed generously of their time in building and maintenance of research facilities. Special thanks to Dr. Robert C. May for his criticism of the manuscript.

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ARGYRIPNUS BROCKI, A NEW SPECIES OF STOMIATOID FISH FROM HAWAII, WITH OBSERVATIONS ON *A. EPHIPPIATUS* AND *A. IRIDESCENS*

PAUL STRUHSAKER[1]

ABSTRACT

Argyripnus brocki is proposed as a new species, and new observations on *A. ephippiatus* from the Hawaiian Islands and *A. iridescens* from Australia are presented. *A. brocki* differs from *A. atlanticus, A. ephippiatus,* and *A. iridescens* in possessing fewer photophores in the VAV + anterior AC series, fewer photophores in the posterior AC series, fewer gill rakers, fewer vertebrae, and a greater interorbital distance. A single small specimen of *Argyripnus* from the Indian Ocean is tentatively assigned to *A. brocki.* Evidence is presented that *Argyripnus* is primarily an inhabitant of the near-bottom community. In Hawaii, *A. brocki* and *A. ephippiatus* exhibit nonoverlapping vertical distributions.

The stomiatoid genus *Argyripnus* is poorly known. At the time of Grey's (1961, 1964) treatments of the group, only 47 specimens of the three nominal species were available for study. Because *Argyripnus* was not present in the open-sea collections of the RV *Dana,* Bruun (according to Grey, 1964) had earlier suggested that members of this genus may live near the bottom. All but 3 of the previously reported 47 specimens have been taken with bottom-fishing gear. The holotype of *Argyripnus atlanticus* Maul 1952 was taken alive at the surface off Madeira, and two specimens were collected after being killed by a lava flow entering the sea from the island of Hawaii (Gosline et al., 1954; Grey, 1961). The later specimens are the only record of *A. atlanticus* from the Indo-Pacific region.

During recent bottom trawling surveys by the NMFS (National Marine Fisheries Service, formerly the Bureau of Commercial Fisheries) in the Hawaiian Islands, numerous individuals of *Argyripnus* were taken and provide additional evidence that the members of this genus are primarily demersal. The material consists of about 460 specimens of *Argyripnus ephippiatus* Gilbert and Cramer 1897 and about 145 specimens of a new species, *A. brocki,* proposed herein. Additional observations on *A. ephippiatus* and *A. iridescens* McCulloch 1926 are also presented. I did not find specimens of *A. atlanticus* in the new Hawaiian material, and taxonomic judgments relative to this species are based on data presented by Grey (1961, 1964).

METHODS

Most sampling was done with 12.5-m (headrope) shrimp trawls (ST) constructed of 38-mm mesh (stretched) webbing in the body and cod end. Limited sampling was also done with similarly constructed 7-m and 21.5-m shrimp trawls. A discussion of the sampling effort and ichthyological results of the surveys is given by Struhsaker (1973).

Measurements were made point to point and generally are as defined by Hubbs and Lagler (1958). Measurements and counts of paired structures are usually the average of both sides. The first and second anal fins are separated at the third photophore of the middle AC series. The last two dorsal and anal rays are counted as two.

Photophore terminology is that of Grey (1964), except that in this case I follow Ahlstrom and Moser (1969) in dividing the IV

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series into the IP (isthmal) and PV (abdominal) groups. All photophores, regardless of how rudimentary, were counted. There are two closely associated gill rakers at the angle of the first arch: The upper one is associated with the epibranchial and is included in the count for the upper limb, while the lower raker is included in the count for the lower limb. The pelvic rays of most specimens of *Argyripnus* I have examined are usually split and can only be counted accurately when submerged in fluid. Most vertebral counts were obtained from radiographs.

As an aid in the analysis of the morphometric characters, measurements obtained for the various body parts of all the specimens of *Argyripnus* I examined were plotted as functions of the standard length (SL) in both original units and as percent of SL.

ARGYRIPNUS BROCKI NEW SPECIES

(Figure 1)

Holotype.—U.S. National Museum (USNM) No. 207653, female, 81.5 mm SL, collected by the NMFS RV *Townsend Cromwell* at station TC-36-24 (*Townsend Cromwell* cruise 36, station 24); north edge Penguin Bank, Hawaiian Islands, lat. 21°09.7′N, long. 157°29.3′W (start of haul), 2235-0028 (local time), 4-5 May 1968, 183 m, 12.5-m shrimp trawl (ST).

Paratypes.—Four specimens (of 10 from station), USNM 207654, 46.5, 50, 52.5, and 56 mm SL, station TC-35-33, north edge Penguin Bank (lat. 12°09.7′N, long. 157°25.0′W) 1912-2052, 7 April 1968, 183 m, 12.5-m ST. One specimen, USNM 207655, 51.2 mm SL, station TC-35-34, north edge Penguin Bank (lat. 21°09.7′N, long. 157°25′W), 2225-2353, 7 April 1968, 183 m, 12.5-m ST. One specimen, USNM 207656, 54 mm SL, station TC-35-35, north edge Penguin Bank (lat. 21°09.7′N, long.157° 24.9′W), 0127-0307, 8 April 1968, 183 mm, 12.5-m ST. One specimen, USNM 207657, 84 mm SL, station TC-35-39, Kalohi Channel (lat. 20°59.3′ N, long. 157°03′W), 1902-2007, 8 April 1968, 274 m, 12.5-m ST. Four specimens (of 21, including holotype), USNM 207658, 64.5, 70.5, 83, and 91.5 mm SL, station TC-36-24, same data as for holotype. Four specimens (of 51) USNM 207659, 64, 65, 80, and 91 mm SL, station TC-36-26, north edge Penguin Bank (lat. 21°09.7′N, long. 157°29.7′W), 0336-0521, 5 May 1968, 183 m, 12.5-m ST. Two specimens, USNM 207660, 66.5 and 75 mm SL, station TC-40-2, north edge Penguin Bank (lat. 21°09.9′N, long. 157°24.1′W), 2144-2344, 6-7 November 1968, 183 m, 12.5-m ST. One specimen, USNM 207661, 77.5 mm SL, station TC-40-16, north edge Penguin Bank (lat. 21°09.8′N, long. 157° 24.5′W), 2021-2205, 8 November 1968, 179 m, 12.5-m ST. One specimen, USNM 207662, 70 mm SL, station TC-40-20, north edge Penguin Bank (lat. 21°09.8′N, long. 157°24.3′W), 2025-2222, 9 November 1968, 12.5-m ST.

Additionally, specimens of *A. Brocki* not included in the type series were taken at the following stations during the surveys: TC-33-15 (1 specimen), Pailolo Channel (lat. 21°01.5′N,

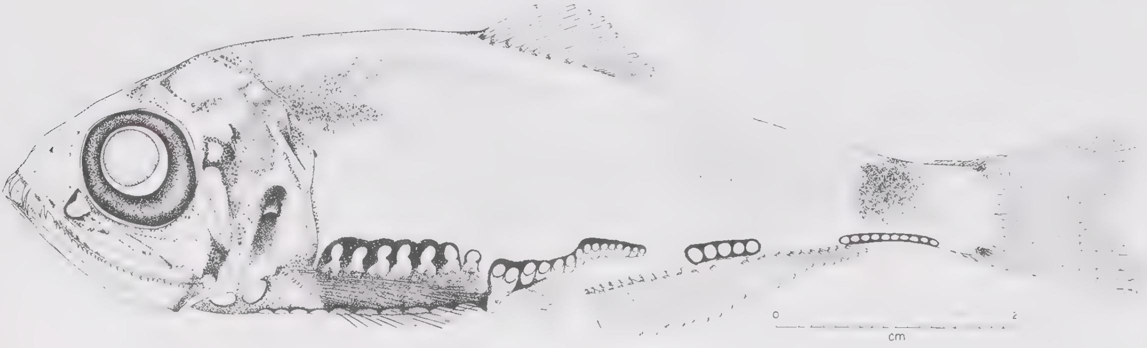

FIGURE 1.—Holotype of *Argyripnus brocki*, USNM 207653.

long. 156°45.9′W), 2028-2228, 31 October 1967, 248 m, 12.5-m ST. TC-33-25 (3), Kealaikahiki Channel (lat. 20°43.3′N, long. 156°48.6′W), 0150-0250, 4 November 1967, 224 m, 8-m ST. TC-33-37 (2), Kealaikahiki Channel (lat. 20°41.7′N, long. 156°39.8′W), 1747-1836, 9 November 1967, 276 m, 8-m ST. TC-35-8 (1), northeast coast Hawaii Island (lat. 19°54′N, long. 155°03.1′W), 1804-1930, 29 March 1968, 280 m, 12.5-m ST. TC-35-36 (1), north edge Penguin Bank (lat. 21°10.2′N, long. 157°24.9′W), 0435-0625, 8 April 1968, 183 m, 12.5-m ST. TC-36-23 (22), north edge Penguin Bank (lat. 21°09.7′N, long. 157°25.2′W), 2019-2149, 4 March 1968, 183 m, 12.5-m ST. TC-36-35 (20), north edge Penguin Bank (lat. 21°09.7′N, long. 157°24.9′W), 0114-0245, 5 May 1968, 183 m, 12.5-m ST. TC-40-10 (7), north edge Penguin Bank (lat. 21°09.8′N, long. 157°24.4′W), 2021-2211, 7 November 1968, 181 m, 12.5-m ST. TC-40-26 (1), north edge Penguin Bank (lat. 21°09.8′N, long. 157°24.2′W), 2023-2124, 10 November 1968, 183 m, 12.5-m ST. TC-40-61 (5), Pailolo Channel (lat. 21°02.1′N, long. 156°44.4′W), 2026-2126, 18 November 1968, 238 m, 12.5-m ST. These specimens, and those taken at the same stations as specimens in the type series, are in the collections of the Southwest Fisheries Center, Honolulu Laboratory, National Marine Fisheries Service, NOAA.

Diagnosis

A. brocki is morphologically closest to *A. ephippiatus* and *A. iridescens*. These three species differ markedly from *A. atlanticus* in having fewer photophores in the VAV + anterior AC series and the posterior AC series. They usually have fewer gill rakers, pectoral rays, and vertebrae (Table 1). They have shorter snouts and longer upper jaws than *A. atlanticus*. The anal fins in *A. brocki*, *A. ephippiatus*, and *A. iridescens* originate below the posterior half of the dorsal fin bases, whereas the anal fin in *A. atlanticus* originates nearly below the origin of the dorsal fin.

Counts. — *A. brocki* exhibits clearcut differences from the three nominal species of this genus in having fewer photophores in the VAV + anterior AC series (17 or less in specimens 40 mm SL or longer, Figure 2, as compared with 18-28), fewer photophores in the posterior AC series (9-11 as compared with 12-18), fewer gill rakers (15-17 as compared with 18-26), and fewer vertebrae (41-43 as compared with 44-46).

Measurements. — *A. brocki* differs from *A. ephippiatus* in possessing a smaller bony orbit, greater interorbital distance, and (in specimens longer than 70 mm SL) a greater distance from snout to anal fin origin. It differs from *A. atlanticus* in possessing a greater interorbital distance, longer snout, longer upper jaw (and accordingly, a longer premaxillary and maxillary), a greater body depth, longer dorsal fin base, and a greater snout to anal fin origin distance. It differs from *A. iridescens* in that it possesses a greater interorbital distance.

Description

Meristics. — The meristics for the 20 specimens in the type series are summarized below and in Table 1. Supplementary counts for certain characters were obtained from specimens not included in the type series. The number of specimens having a particular count is given in parentheses. Occasionally, only one side of bilaterally symmetrical structures could be counted.

Gill rakers on first arch (counts for the right upper and lower limbs given first): 4/4 + 11/11(1), 4/4 + 11/12(1), 4/4 + 12/12(12), 4/5 + 12/12(2), 4/4 + 12/3(2), 5/5 + 12/12(2). The four specimens with five gill rakers on the upper limb were small, being 41-56 mm SL. Pelvic rays: 7(19). Caudal rays (primary): 10 superior, 9 inferior (20). Branchiostegals: 7 + 3 = 10(20).

Only the combined VAV + anterior AC and the posterior AC series of photophores exhibit variation. ORB: 1/1(20). OP: 3/3(20). BR: 6/6(44). IV series — IP: 6/6(43), PV: 10/10 (43). OA: 7/7(44). Middle AC: 5/5(44). Posterior AC 9-11 (Table 1). There is no obvious relation between specimen size and numbers of posterior AC photophores. The number of photophores in the VAV + anterior AC series increases with size until the full complement

TABLE 1.—Summary of meristics of four species of *Argyripnus*. Frequency data are not available for *A. atlanticus* except one vertebral count (Grey, 1964).

Total gill rakers	15	15.5	16	16.5	17	17.5	18	18.5	19	19.5	20	20.5	21	21.5	22	23	24	25	26
A. brocki	1	1	12	4	2	—	—		—	—	—	—	—	—	—	—	-	—	—
A. ephippiatus	—	—	—	—	—	—	2	4	20	4	—	—	—	—	—	—	—	—	—
A. iridescens	—	—	—	-	—	—	—	—	—	—	—	1	6	1	1	—	—	—	-
A. atlanticus	—	—	-		-	-	—	-	-	—	—	—	—	—	+	+	+	+	+

Posterior AC photophores	9	9.5	10	10.5	11	11.5	12	12.5	13	13.5	14	15	16	17	18
A. brocki	1	2	26	5	7	—	—	—	—	—	—	—	—	—	—
A. ephippiatus	—	—	—	—	—	—	2	2	15	1	10	-	—	—	-
A. iridescens	—	—	—	—	—	—	5	—	2	—	1	—	—	—	—
A. atlanticus	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+

Pectoral rays	13	13.5	14	14.5	15	15.5	16	16.5	17	18	19
A. brocki	1	—	9	5	18	—	2	—	—	—	—
A. ephippiatus	—	—	2	3	20	2	1	—	—	—	—
A. iridescens	—	—	—	—	—	—	3	1	5	—	—
A. atlanticus	—	—	—	—	—	—	—	—	+	+	+

Dorsal rays	10	11	12	13
A. brocki	1	21	8	—
A. ephippiatus	—	10	1	—
A. irridescens	—	1	6	2
A. atlanticus	—	+	+	—

First anal rays	10	11	12	13	14	15
A. brocki	1	18	11	—	—	—
A. ephippiatus	—	2	24	3	—	—
A. iridescens	—	—	—	1	6	—
A. atlanticus	—	—	—	+	+	+

Total anal rays	19	20	21	22	23	24	25
A. brocki	2	3	11	12	1	1	—
A. ephippiatus	—	—	1	7	16	5	—
A. iridescens	—	—	—	—	1	2	4
A. atlanticus	—	—	—	+	+	+	+

Second anal rays	8	9	10	11	12
A. brocki	1	4	20	4	1
A. ephippiatus	—	—	8	18	3
A. iridescens	—	—	3	4	—
A. atlanticus	—	+	—	—	—

Total vertebrae	41	42	43	44	45	46
A. brocki	5	17	1	—	—	—
A. ephippiatus	—	—	—	16	2	—
A. iridescens	—	—	—	—	12	5
A. atlanticus	—	—	—	—	—	1

of 14-17 photophores is attained in specimens longer than about 65 mm SL (Figure 2). Counts for specimens in which the two sides varied are given as the average of the two.

Vertebral counts were obtained from the 20 specimens in the type series and three cleared and stained specimens. Frequency of occurrence was as follows (including urostyle): 41 vertebrae (15 precaudal + 26 caudal), 5 specimens; 42 (15 + 27), 17 specimens; 43 (15 + 28), 1 specimen. Of the five specimens with 41 vertebrae, three exhibited double neural and/or haemal spines on the penultimate vertebra. Vertebral counts for *A. ephippiatus* and *A. iridescens* are given below. Only one vertebral count (46 total) is available for *A. atlanticus* (Grey, 1964).

The number of teeth on the maxillary bone of *A. brocki* (as well as *A. ephippiatus* and *A. iridescens*) increases with growth, there being 15-16 teeth at a SL of about 50 mm and 22-30 at about 90 mm. Although *A. brocki*

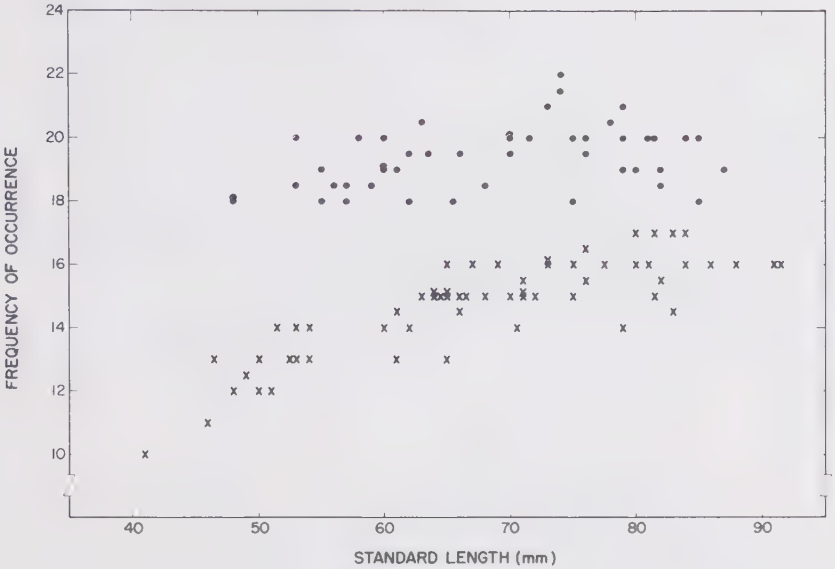

FIGURE 2.—Distribution of VAV + anterior AC photophores by standard length for 60 specimens of *Argyripnus brocki* (X) and 47 specimens of *A. ephippiatus* (dots).

exhibits a significant regression coefficient ($P < 0.001$) for this character, there is much variation ($r^2 = 0.503$) and considerable overlap with the other two species.

In addition to possessing diagnostically fewer VAV + anterior AC photophores, posterior photophores, gill rakers, and vertebrae, *A. brocki* exhibits further differences in numerical characters from the other three nominal species. The range in pectoral-ray numbers (13-16) for *A. brocki* although similar to *A. ephippiatus* (14-16) only slightly overlaps that of *A. iridescens* (16-17) and is less than that of *A. atlanticus* (17-19). The dorsal-ray counts are modally 11 for *A. brocki* and *A. ephippiatus,* while they are 12 for *A. iridescens.* The rays of the first anal fin of *A. brocki* (10-12) are fewer than for *A. iridescens* (13-14) and *A. atlanticus* (13-15), while they are modally one less than for *A. ephippiatus* (11-13). The number of rays in the second anal fin of *A. brocki* is modally one less than those of *A. ephippiatus.* Accordingly, *A. brocki* usually has one to two fewer total anal rays than *A. ephippiatus.*

Measurements. — The original measurements of the 20 specimens in the type series and their range as percent of SL are given in Table 2. Linear regressions were calculated and values for *y*-intercept, regression coefficient, and r^2 are also presented.

A. brocki does not differ greatly from the other species in most of the other body proportions not mentioned in the diagnosis. It does exhibit a strong tendency to be more deeply bodied than *A. ephippiatus.* Comparison with *A. iridescens* is difficult because only larger specimens are available for that species. The adipose fins of *Argyripnus* spp. exhibit considerable variation in the lengths of their bases and distances between their origins and the dorsal fins; much of this variation appears due to mechanical damage. In some specimens the adipose fin is completely missing.

The length-frequency distribution for 123 specimens of *A. brocki* is given in Figure 3. Females longer than 65-70 mm seem to be mature.

Color. — All three species examined have the same basic pigmentation pattern. The patch of black pigmentation on the upper portion of the body just behind the head is very seldom entire in specimens of *A. brocki* and *A. ephippiatus* because of chafing in the trawl, but it still appears that this patch is best developed in

TABLE 2.—*Argyripnus brocki*: Measurements (mm), ranges of proportions (percent SL), *y*-intercept (*a*), regression coefficient (*b*), and r^2 for the type series.

Standard length (mm)	46.5	50	51.2	52.5	54	56	64	64.5	65	66.5	70	70.5	75
Head length	14.5	16.6	16.0	16.0	16.5	16.5	19.0	20.6	20.6	20.0	21.0	21.8	21.5
Snout length	4.4	4.0	4.6	4.4	4.4	5.0	5.0	5.6	5.8	5.8	5.5	6.0	5.9
Orbit diameter	6.0	6.6	6.5	6.5	6.4	6.4	7.8	8.1	8.0	7.8	8.7	9.0	9.2
Interorbit width	3.8	4.0	4.2	3.8	3.8	4.2	5.0	5.2	5.0	5.2	5.2	5.9	5.4
Length of upper jaw	11.0	11.4	11.5	11.2	12.0	12.2	14.5	15.6	15.0	15.0	16.0	16.5	17.0
Length of premaxillary	5.0	5.8	5.0	5.5	5.5	6.0	6.5	6.5	7.0	7.6	7.8	7.0	7.5
Length of maxillary (toothed portion)	7.0	7.4	8.0	7.2	8.0	7.8	9.2	10.0	9.6	9.0	10.2	11.5	11.2
Greatest body depth	13.4	14.8	16.0	14.2	15.0	15.0	19.0	18.2	19.0	19.0	21.0	21.0	22.5
Least depth caudal peduncle	4.9	5.0	5.2	4.9	5.6	5.5	7.0	6.6	6.8	7.0	7.0	7.5	7.2
Length of pectoral fin	11.8	14.0	13.0	12.8	13.6	13.4	15.0	16.6	16.2	16.0	16.0	18.0	17.0
Length dorsal fin base	6.6	7.8	7.2	7.4	7.2	7.5	9.1	8.8	8.8	9.0	9.5	9.8	10.0
Length anal fin base	14.5	16.2	16.4	16.2	16.0	17.2	17.2	20.0	18.2	19.5	18.6	20.5	21.0
Length adipose fin base	5.0	5.2	4.0	—	—	4.0	—	5.8	4.4	—	3.6	—	—
Distance: dorsal to adipose	6.0	9.0	7.0	—	—	10.5	—	11.6	13.5	—	15.2	—	—
Snout to:													
Pectoral fin origin	13.2	14.8	15.5	15.0	15.0	16.0	19.0	19.0	19.0	19.4	20.0	20.4	22.0
Dorsal fin origin	22.0	24.0	24.5	25.5	25.0	26.0	31.5	31.0	32.0	31.0	32.8	34.4	35.0
Anal fin origin	26.0	28.0	28.6	28.8	29.5	31.0	35.0	38.0	36.5	39.0	40.0	40.5	46.0

Standard length (mm)	77.5	80	[1]81.5	83	84	91	91.5	Range percent SL	*a*	*b*	r^2
Head length	24.0	23.6	25.4	27.0	25.0	28.0	28.2	28.7-33.2	0.44	0.301	0.970
Snout length	6.5	6.4	7.0	7.0	7.4	7.8	7.8	7.8- 9.5	0.19	0.082	0.948
Orbit diameter	8.9	9.0	10.0	10.6	9.6	11.0	10.4	11.3-13.2	0.85	0.109	0.948
Interorbit width	6.2	6.0	6.0	6.6	6.8	7.2	7.0	7.0- 8.4	-0.03	0.078	0.952
Length of upper jaw	19.0	18.0	19.0	20.0	20.0	22.0	21.5	21.3-24.5	-1.60	0.255	0.983
Length of premaxillary	8.0	7.0	7.9	8.1	8.0	9.0	8.8	8.8-11.6	1.33	0.082	0.897
Length of maxillary (tooth portion)	12.2	12.0	12.6	13.6	13.2	14.8	14.2	13.5-16.4	-1.57	0.17	0.964
Greatest body depth	23.0	23.5	23.0	27.0	26.0	27.5	27.0	26.8-32.5	-2.02	0.324	0.967
Least depth caudal peduncle	7.2	8.0	7.8	8.5	8.2	8.8	9.0	9.3-10.9	0.55	0.092	0.954
Length of pectoral fin	19.0	17.5	19.5	18.5	20.0	21.0	21.5	21.9-28.0	2.90	0.198	0.939
Length dorsal fin base	11.0	11.5	11.9	11.5	12.0	12.5	13.0	13.3-15.6	-0.04	0.140	0.973
Length anal fin base	23.4	22.0	23.0	23.2	23.0	25.0	25.0	26.6-32.4	4.15	0.228	0.947
Length adipose fin base	5.5	6.1	6.0	8.1	6.0	5.0	7.0	5.1-10.8	2.07	0.047	0.349
Distance: dorsal to adipose	14.5	15.0	15.0	13.5	15.0	16.6	19.0	12.9-21.7	6.94	0.114	0.205
Snout to:											
Pectoral fin origin	23.0	23.0	24.0	25.2	26.0	28.0	27.2	27.8-31.0	-1.58	0.317	0.989
Dorsal fin origin	38.0	39.5	40.8	42.0	41.0	45.0	45.0	46.3-50.6	-2.52	0.521	0.990
Anal fin origin	46.0	47.0	49.5	50.2	50.0	55.8	55.0	54.6-61.3	-6.52	0.677	0.992

[1] Holotype.

A. iridescens. The black patch on the caudal peduncle is best developed in *A. brocki,* less so in *A. ephippiatus,* and is weakest in *A. iridescens.* Some specimens of *A. iridescens* possess pigmentation on the distal portions of the dorsal rays, a condition not observed in the other two species. In fresh specimens of *A. brocki* and *A. ephippiatus,* the body musculature is translucent.

Etymology. — Named for the late Vernon E. Brock in recognition of his contributions to marine biology and his encouragement and support of my studies on Hawaiian bathyal fishes.

ARGYRIPNUS EPHIPPIATUS GILBERT AND CRAMER

Measurements and counts were obtained from the following material: 12 specimens (of 256), USNM 207663, 53-87 mm SL, station TC-33-29, Kealaikahiki Channel (lat. 20°35.0′ N, long. 156°50.9′W), 1915-2100, 4 November 1967, 412 m, 7-m ST. Three specimens (of 189) USNM 207664, 62-78 mm SL, station TC-33-30, Kealaikahiki Channel (lat. 20°34.1′N, long. 156°52.2′W), 0010-0210, 5 November 1967, 400 m, 7-m ST. *A. ephippiatus* was taken at eight

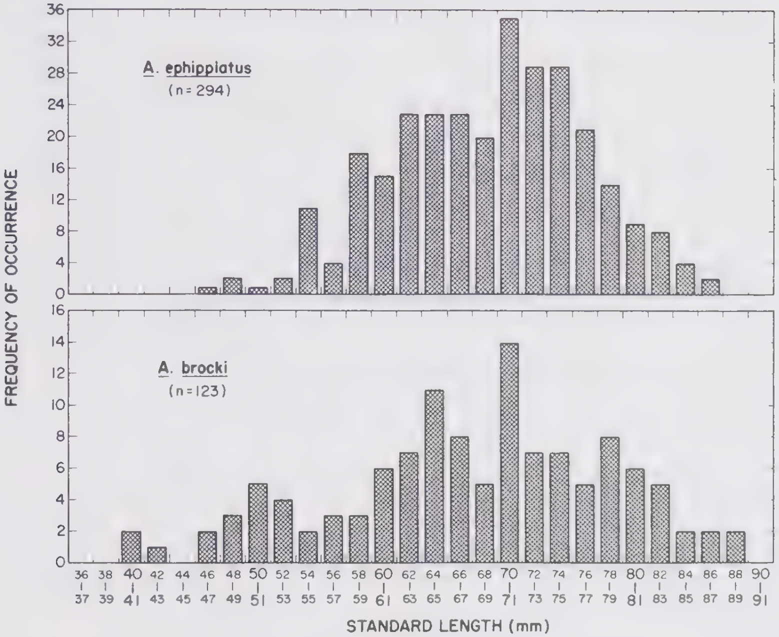

FIGURE 3.—Length-frequency distributions for 123 specimens of *Argyripnus brocki* and 294 specimens of *A. ephippiatus*.

additional stations (2-8 specimens per station), all in the 325- to 450-m depth range.

Measurements obtained from the 15 specimens are given in Table 3, while some of the counts (supplemented by randomly selected individuals from the same stations) are summarized in Table 1. The length-frequency distribution for 294 specimens is given in Figure 3. As in the case of *A. brocki*, *A. ephippiatus* females longer than 65-70 mm seem to be mature.

Gill rakers on the first arch: 5/5 + 13/13(2), 5/5 + 13/14(4), 5/5 + 14/14(20), 5/5 + 14/15(2), 6/5 + 14/14(2). Pelvic rays: 7(13). Caudal rays (primary): 10 superior and 9 inferior (9). Branchiostegals: 7 + 3 = 10(15).

ORB: 1/1(15). OP: 3/3(15). BR: 6/6(15). IV series — IP: 6/6(12), PV: 10/10(12). OA: 7/7(15). Middle AC: 4/4(1), 5/5(28). Posterior AC: 12-14: (Table 1). There was no obvious relation between specimen size and number of posterior AC photophores. The number of VAV + anterior AC photophores (18-22) also increases with growth in *A. ephippiatus*, although the variation within the observed size range is not as pronounced as for *A. brocki*. The linear regression coefficient obtained for the photophore-SL relations for 47 specimens of *A. ephippiatus* (Figure 2) is significant ($P < 0.01$, but r^2 is only 0.145).

Total vertebrae for 18 specimens ranged from 44 to 45: 14 precaudal + 30 caudal, 2 specimens; 15 + 29, 14 specimens; 15 + 30, 2 specimens.

ARGYRIPNUS IRIDESCENS McCULLOCH

I have examined nine specimens of McCulloch's type series deposited in The Australian Museum. Each specimen is individually tagged, and the measurements I obtained from them are given in Table 4. Some of the counts are summarized in Table 2.

Gill rakers: 6/6 + 14/15(1), 6/6 + 15/15(6), 7/7 + 15/15(1), 6/6 + 15/16(1). Pelvic rays: 7(9). Caudal rays: 10 superior, 9 inferior (9). Branchiostegal rays: 7 + 3 = 10(9).

TABLE 3.—*Argyripnus ephippiatus:* Measurements (mm), range of proportions (percent SL), *y*-intercept (*a*), regression coefficient (*b*), and r^2 for 15 specimens.

Standard length (mm)	53	62	63	65.5	66	70	71.5	73	74	75	76	78	79	81.5	87	Range percent SL	*a*	*b*	r^2
Head length	17.4	20.6	22.0	21.0	20.0	20.4	24.0	22.0	22.2	24.4	23.5	24.0	27.0	24.0	27.0	29.1-34.9	3.57	0.266	0.787
Snout length	5.0	5.0	5.2	5.2	5.2	5.5	5.8	5.6	6.0	6.6	6.2	5.8	6.4	6.1	6.5	7.4- 9.4	1.29	0.055	0.761
Orbit diameter	7.6	9.0	9.3	9.4	9.0	9.6	10.2	10.0	10.0	10.2	10.7	11.0	11.6	11.5	12.0	13.5-14.8	0.70	0.131	0.945
Interorbit width	3.3	3.8	3.5	3.6	3.6	3.9	4.7	4.6	4.2	5.0	4.8	5.0	4.5	5.1	—	5.5- 6.7	-0.78	0.071	0.787
Length of upper jaw	12.8	15.2	15.8	15.5	15.9	16.8	17.0	16.8	16.8	18.1	17.5	17.6	18.6	19.0	21.0	22.6-25.1	1.74	0.212	0.945
Length of premaxillary	6.3	7.0	7.6	7.0	7.0	7.8	8.0	8.0	8.0	8.2	8.0	8.0	8.5	8.0	8.4	9.7-12.1	3.14	0.064	0.804
Length of maxillary (toothed portion)	8.0	10.1	10.2	10.0	10.9	11.0	11.5	11.0	10.8	11.2	11.2	12.2	12.5	13.0	14.0	14.6-16.5	0.03	0.156	0.907
Greatest body depth	14.6	17.8	18.0	17.0	17.8	20.0	20.0	20.0	19.5	20.0	20.0	21.0	22.6	21.6	25.2	26.0-28.9	-0.05	0.275	0.909
Least depth caudal peduncle	4.9	5.8	6.2	5.8	6.2	6.3	6.8	6.8	7.0	6.3	6.4	7.2	7.7	7.8	7.5	8.4- 9.8	0.63	0.083	0.828
Length of pectoral fin	13.0	14.5	16.2	16.5	17.0	18.0	17.2	18.0	17.8	17.0	18.5	17.0	19.6	19.0	21.0	21.8-25.8	2.58	0.206	0.845
Length dorsal fin base	—	7.8	7.5	8.4	8.0	9.5	8.4	9.0	9.0	10.0	9.2	10.0	10.0	11.0	—	11.7-13.6	-1.77	0.151	0.841
Length anal fin base	17.0	20.0	20.0	21.0	21.5	22.0	23.0	24.0	22.0	24.5	23.0	26.0	25.5	25.5	27.0	29.7-33.3	1.25	0.301	0.930
Length adipose fin base	—	—	—	—	—	—	6.2		—	—	—	8	—	—	—	8.7-10.3	—	—	—
Distance:dorsal to adipose	—	—	—	—	—	—	13.0	—	—	—	—	12	—	—	—	15.4-18.2	—	—	—
Snout to:																			
Pectoral fin origin	16.0	18.0	19.3	18.8	20.0	20.0	21.0	20.6	22.4	22.0	22.8	22.2	23.8	23.9	27.0	28.2-31.0	-0.63	0.305	0.945
Dorsal fin origin	24.5	29.0	29.0	29.6	30.0	32.2	33.5	33.0	35.5	36.0	34.5	36.0	38.8	37.5	41.5	45.2-49.1	-2.49	0.499	0.965
Anal fin origin	29.0	33.5	35.0	36.0	36.5	38.0	39.5	40.0	41.5	40.0	41.8	42.4	42.0	44.0	47.5	53.0-56.5	1.38	0.527	0.985

Counts for the ORB, OP, BR, IP, and PV series are as for other species of *Argyripnus.* VAV + anterior AC: 19.5(2), 20(7). Middle AC: 5(9). Posterior AC 12-14 (Table 1).

Total vertebrae for 17 specimens (radiographs obtained for 8 unexamined specimens) ranged from 45 to 46: 15 precaudal + 30 caudal, 12 specimens (including holotype); 15 + 31, 3 specimens; 16 + 30, 2 specimens.

McCulloch (1926) stated that *A. iridescens* was so similar to *A. ephippiatus* that he separated the two species with hesitation. The new counts presented here for the two species indicate that they should continue to be recognized.

ARGYRIPNUS SPP.

I have examined the following three specimens of *Argyripnus:* (1) 51 mm SL, USNM 207984. RV *Anton Bruun* cruise 9, station 422, Indian Ocean, lat. 6°51′N, long. 39°54′E, 19 November 1964, 100 m, midwater trawl. (2) 64 mm SL, SIO 69-19-10 (Scripps Institution of Oceanography Circe Expedition, Celebes Sea), lat. 06°00′N, long. 122°36′E, 21 April 1968, midwater trawl. (3) USNM 135402, 78 mm SL. This is the same Philippine specimen treated by Grey (1961).

Measurements obtained on selected body parts are given in Table 4. Counts that were obtained on characters that show variation in other species of *Argyripnus* are as follows (values given are for the respective specimen number). VAV + anterior AC photophores: 15, 16, 18. Posterior AC photophores: 10, 11, 12. Gill rakers: 4/4 + 11/11, 4/4 + 12/12, 2/4 + 9/12. There is no indication that the right gill arch has been damaged on the third specimen, but the higher count is taken to be "correct." Pectoral rays: 15, 17, 15. Dorsal rays: ca. 13, 12, 10. First anal rays: ca. 11, 13, 11. Second anal rays: ca. 9, 10, not available.

TABLE 4.—Measurements (mm) of nine *Argyripnus iridescens*, one *A. brocki* from the Indian Ocean (USNM 207984), and two specimens of undetermined species of *Argyripnus* (last two columns).

Specimen number	IA1347	IA1346	E4369	IA1345	E6586	E6584	IA1344	IA1349	IA1348	Range percent SL	USNM 207984	SIO 69-19-10	USNM 135402
Standard length (mm)	83.5	85	98	98	98.5	101	104	108	112	—	51	64	78
Head length	26.0	26.0	28.0	31.0	29.5	30.5	32.0	32.3	34.0	28.6-31.6	16.5	19.7	27.0
Snout length	7.0	6.6	7.5	7.0	7.6	8.0	8.0	8.2	9.5	7.1- 8.5	4.4	5.2	7.0
Orbit diameter	10.0	11.0	12.0	11.6	12.4	12.2	13.0	12.8	14.0	11.8-12.9	6.9	7.8	11.8
Interorbit width	5.4	5.2	5.9	6.0	6.0	6.0	6.8	7.0	7.0	5.9- 6.5	3.2	4.1	5.8
Length of upper jaw	18.6	18.0	21.8	21.0	21.5	23.0	23.0	23.6	25.0	21.2-22.8	12.5	15.0	19.0
Length of premaxillary	8.0	8.0	9.0	8.5	7.8	10.0	9.8	9.4	9.5	7.9- 9.9	6.0	5.8	9.0
Length of maxillary (toothed portion)	12.6	12.6	14.5	14.9	15.0	15.0	16.0	16.2	17.0	14. -15.4	8.0	11.0	13.0
Greatest body depth	21.5	23.0	27.5	27.0	26.0	30.0	30.0	31.9	32.5	25.7-29.5	15.0	18.0	22.0
Least depth caudal peduncle	7.8	8.0	9.0	8.1	8.8	—	9.2	9.6	10.0	8.3- 9.4	5.0	6.1	7.4
Length of pectoral fin	20.0	21.0	23.0	23.0	22.5	23.0	24.0	24.5	26.5	22.8-24.7	12.0	—	17.0
Length dorsal fin base	11.3	11.0	12.2	13.0	13.0	13.0	13.0	15.0	14.2	12.4-13.9	9.0	9.0	12.0
Length anal fin base	27.7	27.0	29.5	32.0	31.0	31.0	30.0	35.0	37.0	28.8-33.2	15.0	20.0	26.0
Length adipose fin base	4.2	7.0	6.2	6.0	9.0	9.0	8.0	6.8	5.5	4.9- 9.1	—	—	—
Distance: dorsal to adipose	14.6	14.0	18.0	15.0	17.0	18.0	19.0	17.0	18.0	15.3-18.4	—	—	—
Snout to:													
Pectoral fin origin	23.0	23.0	29.0	29.0	27.5	29.5	28.5	30.0	32.2	27.1-29.6	15.0	19.2	25.0
Dorsal fin origin	40.0	41.0	48.0	48.0	48.5	50.0	52.0	51.0	55.0	47.2-50.0	23.5	29.0	39.0
Anal fin origin	46.5	47.0	55.0	57.0	56.0	57.0	61.0	61.0	64.0	55.3-58.7	27.0	—	45.0

Vertebrae: 42 (15 precaudal + 27 caudal), 44 (15 + 29), 44 (15 + 29).

I tentatively assign the 51-mm specimen from the Indian Ocean to *A. brocki*. The specimen shares in common with the Hawaiian type series 19 of 23 morphological and meristic characters, including the four diagnostic counts (VAV + anterior AC photophores, posterior AC photophores, gill rakers, and vertebrae). It does not agree with the range of interorbital measurements obtained from the type series (a diagnostic character), but this may be due to geographical variation or distortion of the small specimen. Thus, the distribution of *A. brocki* may extend from Hawaii to the Indian Ocean.

Although the remaining two specimens certainly do not represent *A. atlanticus*, I cannot definitely assign them to a species because, to varying extents, they share characters with *A. brocki*, *A. ephippiatus*, and *A. iridescens*. For example, the Philippine specimen exhibits 10 body proportions similar to both *A. ephippiatus* and *A. brocki*, 3 proportions characteristic of *A. ephippiatus*, and 3 proportions characteristic of *A. brocki*. With regard to counts, there are two characters common to both *A. ephippiatus* and *A. brocki*, one common to *A. ephippiatus*, two common to *A. brocki*, and one shared by both *A. ephippiatus* and *A. iridescens*.

While this report was in press I had the opportunity to examine an approximately 60-mm SL specimen of an undetermined species of *Argyripnus* taken from the stomach of a specimen of *Etelis* captured at a depth of 280 m outside of "Grand Récif," New Caledonia. The specimen is in poor condition and only the vertebrae and gill rakers may be counted with certainty. The total vertebral count of 42 (14 + 28) places this specimen within the range of vertebral counts for *A. brocki*. However, the only *Argyripnus* specimens I have examined that possess 14 precaudal vertebrae are two individuals representing *A. ephippiatus* (all other specimens have 15 or 16 precaudal vertebrae). The gill raker count of 3 + 10 = 13 (for both sides) is two less than the lowest count obtained for *A. brocki* (which has the lowest gill raker counts of the four species treated here). The stomach of the New Caledonia *Argyripnus* specimen contains an undetermined myctophid. I thank P. Fourmanoir and Robert K. Johnson for making this specimen available for study.

ECOLOGY

The capture of large numbers of *Argyripnus* in bottom-fishing gear strongly indicates that the genus is essentially a member of the near-bottom (demersal, engybenthic) bathyal ichthyofauna. In the case of the Hawaiian specimens reported here, it seems improbable that such large numbers of *Argyripnus* would be taken during the short periods of time that the bottom-fishing trawls are effectively sampling the midwater environment. This premise is argued for by the absence of the genus in the numerous midwater trawl stations occupied by NMFS and the University of Hawaii (Thomas A. Clarke, pers. comm.) within a few miles of the Hawaiian Islands. Additionally, if the species were pelagic and being captured during the setting and hauling of the trawl, then they would be expected to be present in all the deeper hauls, including those exceeding the apparent optimal depths of the two species as indicated by the data presented here. The two specimens taken in the Indian Ocean and the Celebes Sea by midwater trawls are most likely individuals that have been displaced from the bathyal environment. If the young of this genus are pelagic like other stomiatoids, it should not be surprising to occasionally encounter a small specimen offshore. However, the possibility of established breeding populations of the genus in the oceanic realm cannot be ruled out at present.

A. brocki and *A. ephippiatus* were never taken in the same trawl haul. The capture records show that the vertical distributions of the two species do not overlap: *A. brocki* was taken at 17 stations in depths of 180-280 m, while *A. ephippiatus* appeared at 10 stations in depths of 325-450 m. This must be one of the few examples of sympatric congeneric bathyal fish species not exhibiting some degree of overlap in their vertical distributions.

A. brocki and *A. ephippiatus* were never taken between dusk and dawn. Possibly this species undergoes diel vertical migrations over the sea bottom as has been hypothesized for several other species of Hawaiian bathyal fishes (Struhsaker, 1973). Because of the relatively small numbers of specimens taken, however, the effect of net avoidance during daylight hours cannot be discounted at present.

ACKNOWLEDGMENTS

I thank John C. Marr and Richard S. Shomura for the opportunity to examine the study material. John R. Paxton made available specimens and radiographs of *A. iridescens* from The Australian Museum. Other radiographs were provided by Scripps Institution of Oceanography and the Systematics Laboratory, NMFS. Richard H. Rosenblatt and Robert K. Johnson loaned the specimen of *Argyripnus* from the Celebes Sea and reviewed the manuscript. I am indebted to Robert H. Gibbs, Jr., and Stanley H. Weitzman for review of the manuscript. The illustrations are by Tamotsu Nakata. Much of this work was supported by the Hawaii Institute of Marine Biology, University of Hawaii, and is HIMB contribution No. 393.

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7332

EXPLORATORY SHRIMP TRAPPING
IN THE HAWAIIAN ISLANDS

BY

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Introduction

During 1967 and 1968 the National Marine Fisheries Service (NMFS) devoted four cruises of the RV *Townsend Cromwell* to demersal resource surveys in the Hawaiian Islands. The primary sampling gears utilized were shrimp trawls, although limited shrimp trapping experiments were conducted (Yoshida, 1972). These surveys demonstrated that the penaeid shrimp (*Penaeus marginatus*) was available in modest amounts and amenable to harvest by shrimp trawls. Two species of caridean shrimps (*Heterocarpus ensifer* and *H. laevigatus*) were also taken in small numbers with the trawls. However, the initial investigations indicated that trapping, rather than trawling, was a more effective method for harvesting these latter species.

Clarke (1972) conducted trapping surveys during 1969 and 1970 at seven locales off Oahu, Hawaiian Islands. The sampling gear consisted of several trap types, but all were uncovered traps. These surveys provided data on the depth distributions of *H. lensifer* and *H. laevigatus* and indicated that these species were present in sufficient quantities to support a commercial fishery.

Further trapping trials were conducted by the NMFS during fall, 1972 at various localities in the main group of the Hawaiian Islands. These trials were of preliminary nature, and a variety of trap types, bait containers, and baits was utilized. It was demonstrated at this time that traps covered with burlap were more effective in capturing *H. ensifer* than were uncovered traps. It was also determined that proper catch preservation of this species was essential to insure a quality product.

We also have data from 23 sets of our gear off Oahu by staff members of the Hawaii Institute of Marine Biology, University of Hawaii during May 1973.

Methods

The traps measure 2 by 2 by 4 ft. The frame is constructed of 3/8-inch diameter steel bar and is covered with 1/2-inch square mesh galvanized wire screen. The sides, top, and bottom are then covered with burlap. The tunnels (one at each end) are also constructed with the screen (but are uncovered) and taper to 2- to 3-inch openings about one-third the distance in from each end. Bait containers are constructed with 1/2-inch wire screen and are suspended in the trap between the two tunnel entrances. One to two pounds of chopped bait are sufficient for sets of 12-14 hours.

Each trap has a 7-ft wire bridle attached to opposite corners on the top of the trap. The bridle has a snap at the center for attachment to the ground line. The ground lines and buoy lines consist of 1/2-inch polypropylene rope. The traps are spaced at 10-fathom intervals, and the first and last traps on a string have 5-pound anchors attached to a trap corner. We usually fished six or eight traps to a string, but this would vary according to the capabilities of the vessel. We have our buoy lines made up into 100-fathom lengths, and these are stored in plastic garbage containers of approximately 40-gallon capacity. The ground line is made up with this line by forming loops for each trap at 10-fathom intervals in the distal portion of the first 100-fathom section. The proper number of 100-fathom sections are then added as the traps are set in order to give an excess amount of buoy line on the order of 50-150 fathoms greater than the depth of water being fished. Just before the entire amount of line is payed out, a buoy is attached and set as the final few fathoms are run out. A weight is smapped onto the buoy line about 10 fathoms below the buoy to assure that the polypropylene line does not float at the sea surface. The set is retrieved with a Marco* crab-pot hauler; the 100-fathom sections are stowed directly into their containers as the line comes aboard.

Because the trapping operations were interspersed with other vessel programs, the traps were set at dusk and retrieved at dawn. We do not have data on daytime catch rates.

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* Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Results

Different types of traps, bait containers, and baits were tested by various combinations of these factors on sets of four to eight traps per string. Traps measuring 1 by 2 by 4 ft were less effective than the larger traps measuring 2 by 2 by 4 ft. Traps with 1-inch mesh wire screening caught fewer H. ensifer (through escapement) than those with 1/2-inch mesh screening. Comparison between alternated covered and uncovered traps during eight sets of four to six traps resulted in the covered traps outfishing the uncovered traps by 2.5-10 times. Possibly the covering on the sides of the trap concentrates the bait scent near the entrances at the ends of the traps, resulting in greater catch rates. Quite probably traps constructed of any material that conforms to the basic design principle of the covered trap would be equally effective.

Several bait container types were tested. Containers constructed of 1/2-inch mesh screening (measuring 6 by 6 by 6 inches) were generally superior to plastic containers of the same size perforated with 1/4-inch holes or bait wrapped in cheesecloth.

Five types of bait were tested: finely ground fish, squid, shrimp (H. ensifer) and coarsely chopped fish and shrimp. Chopped fish species that are lily or bloody were found to be the best baits. Possibly the fine-ground baits dispersed to rapidly. Fish and shrimp were superior to squid.

Catch rates of H. ensifer obtained during 1972 were highly variable due to the variety of traps, bait containers, baits utilized and depths sampled. At this time the best catches ranged between 15 and 63 pounds per trap for an overnight set.

More reliable data on catch variability was provided by 21 sets of covered traps (four per set) off the sough coast of Oahu in depths of 200-220 fathoms during spring, 1973. Only one bait type (fish) was utilized. During this series of sets catches of H. ensifer ranged from 2 to 34 pounds per trap and averaged 15.2 pounds per overnight set. Considerable variation in catch rates between localities was noted.

These catches of H. ensifer with covered traps generally exceeded those experienced by Clarke (1972) off the northeast coast of Oahu with uncovered traps. Catches there for nine sets in the 150-250 fathom depth range varied from 0.6 to 11.9 pounds per trap and averaged 4.5 pounds.

The larger H. laevigatus is apparently much less abundant than H. ensifer. Our usual catches of H. laevigatus were 1-3 pounds, but occasionally ranged up to 9 pounds per trap. Clarke (1972) experienced similar catch rates.

The model size group of H. ensifer retained by the 1/2-inch mesh traps range from 35 to 45 individuals per pound (heads on). The largest individuals of H. laevigatus range from 8 to 12 per pound. For both species the tail (with shell) comprises about 45% of the total body weight.

Clarke (1972) found that H. ensifer occurs in depths of 80-400 fathoms in the Hawaiian Islands, but is most abundant between 150 and 250 fathoms. Shrimps taken in this latter depth range were found to be significantly larger than those taken at the upper and lower limits of the total depth range. H. laevigatus occurred in depths of 200-400 fathoms; there was no obvious trend in abundance between 250 and 400 fathoms. Our fingings during all surveys are in accord with these results. The optimal depth range for H. ensifer corresponds to bottom temperatures of 7 -13 C.

The traps have been fished on a variety of bottom types. The only constraints are that the slope must be gentle enough to permit the traps to fish without drifting off and the bottom must be smooth enough to abviate trap loss.

Attempts to market the two species of Heterocarpus in Hawaii have been generally unsuccessful in the past. This is due to enzymatic breakdown of the chilled tail meat within 12-24 hours which results in a soft and unacceptable product when cooked. We found that cooking the shrimp immediately after catching resulted in a chilled shelf life of 3-4 days. One test of immediate freezing of raw shri;p in a brine solution at about -20 C. resulted in a superior product. After brine freezing, the shrimp were placed in a conventional freezer and tested at intervals over a 2-week period and found to be very acceptable. Very lettle salt was taken up by the shrimps during brine freezing.

Care must be taken not to overcook these species. Boiling times of 2-4 minutes are adequate for the frozen shrimp. The tail meat can be shelled easily for other methods of preparation by briefly thawing with running water.

H. ensifer is known to occur in tropical waters from the western Atlantic to Hawaii. This species, and/or a congener undoubtedly occurs in areas of the South Pacific. The standing biomass of H. ensifer has been greatly underestimated in the past because shrimp trawls appear to be inadequate sampling devices for this purpose. If members of this genus are as abundant in other regions of the tropics as in Hawaii, together they probably represent a biomass exceeding that of any commercially exploitable tropical crustacean.

7333

TUNA: Pole-and-Line Fishing Trials In Central and Western Pacific

R.N. Uchida and R.F. Sumida

The growing interest of the U.S. tuna fishing industry in the development of resources outside the Inter-American Tropical Tuna Commission's regulatory area in the eastern Pacific created an urgent need to assess the tuna-harvesting potential of the central and western Pacific Ocean.

This article presents quantitative baiting and fishing data obtained aboard the Honolulu-based pole-and-line fishing vessel 'Anela'. The vessel explored the possibility of developing commercial fisheries for surface schooling tuna in the Marshalls and American Samoa under a charter of the National Marine Fisheries Service (NMFS).

Anela found the tuna resources in the Marshalls and American Samoa impressive. Bait was plentiful in the Marshalls but scarce in American and Western Samoa. To conduct fishing trials in American Samoan waters, Anela caught bait in Fiji. Both tuna and bait were abundant around Fiji.

The M/V Anela was built in 1971 for the Angel Fishing Company of Honolulu. It was designed for pole-and-line fishing with live bait. It prospected for tuna from February 8 to May 9, 1972, in the central and western tropical Pacific--more particularly in waters of the Marshall Islands and American Samoa.

Anela was chartered by NMFS Southwest Fisheries Center, Honolulu Laboratory, under a formal contract with the Angel Fishing Company. Its mission was to explore the possibility of developing commercial pole-and-line fisheries for skipjack tuna, Katsuwonus pelamis, in the Marshalls and American Samoa. These two areas have been under consideration as potential bases for skipjack fishery development by the PIDC (Pacific Islands Development Commission). The Commission consists of the chief executives of the Governments of Hawaii, American Samoa, Guam, and the Trust Territory of the Pacific Islands. It was formed for cooperative economic development.

The contract stipulated that 20 fishing and baiting days be expended in the Marshalls--10 days (or fewer if a full catch load was obtained in less time) on the outward leg of the cruise, and the balance on the homeward leg. The remaining fishing and baiting time was to be used near American Samoa. Time was allowed for traveling to and from the areas of operation, unloading the catch loading provisions, and refueling. Allowance also was made for days the vessel could not fish because of bad weather.

The contract stated that observers from NMFS the Marshall Islands District of the Trust Territory, and the Government of American Samoa were to be accommodated on the vessel.

ANELA'S SPECIFICATIONS

Anela is the most recent addition to the Hawaii skipjack fishing fleet (Fig. 1). Propelled by an 850-hp Caterpillar[1] D398 engine,

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[1] Use of trade names throughout this article does not imply endorsement by the National Marine Fisheries Service.

MARINE FISHERIES REVIEW
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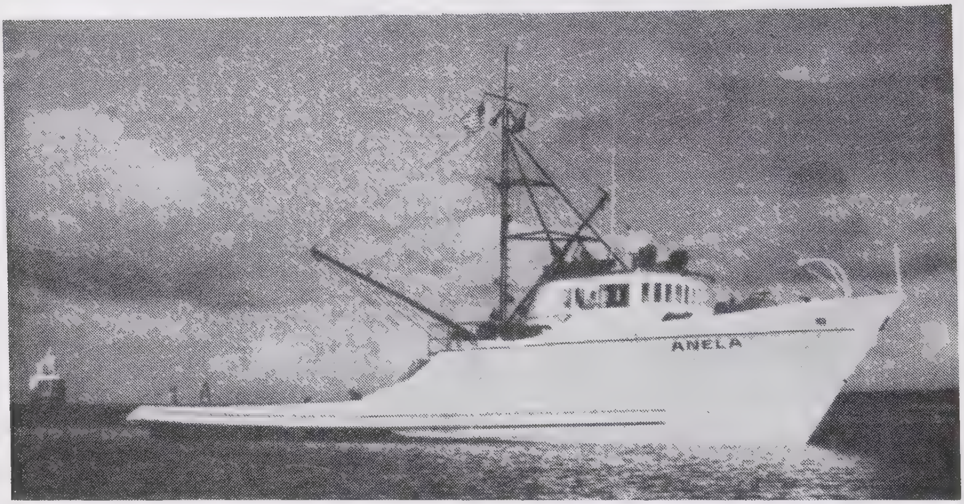
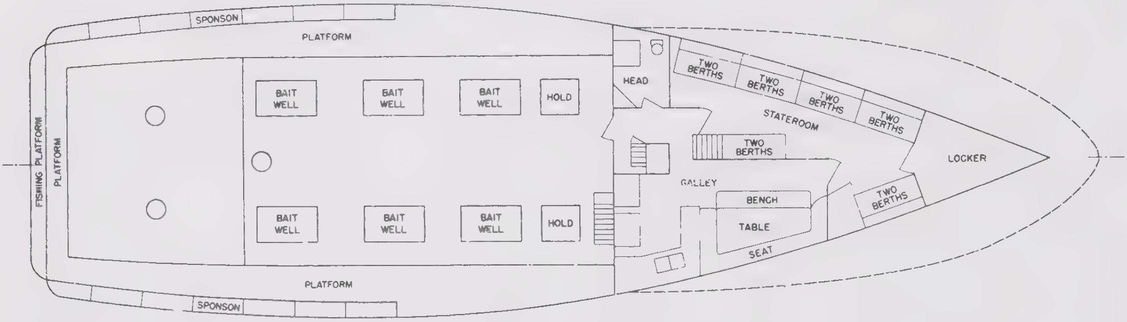


Fig. 1 - 'Anela' anchored in Majuro Lagoon, Marshall Islands.


SPONSON
PLATFORM
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LOCKER
GALLEY
BENCH
TABLE
TWO BERTHS
BAIT WELL
BAIT WELL
BAIT WELL
HOLD
SEAT
PLATFORM
SPONSON

Fig. 2 - Main deck arrangement of 'Anela.'

the steel-hulled vessel has a cruising speed of 13.8 knots and a cruising range of 3,700 km. The registered length is 26.6 m., the beam 7.6 m., and the depth 3.6 m. Gross and net tonnages are 136 and 91 M.T., respectively. The vessel has a fuel-oil capacity of 56,775 liters and freshwater capacity of 11,355 liters.

Figure 2 shows Anela's deck arrangement. The six baitwells, equipped with pump-circulating systems, can hold as much as 160 buckets of bait. When emptied of bait, the baitwells serve as refrigerated fishholds with a fish-carrying capacity of about 77 M.T. Two forward holds are used to store provisions.

MARSHALL ISLANDS (FEB. 16-29)

Departing on the outward leg from Honolulu on February 8, Anela first stopped at Majuro in the Marshall Islands. These islands lie 3,700 km southwest of the Hawaiian Islands on a northwest-southeast axis from lat 15° to 5° N between long 162° and 173° E. The Marshalls make up one of six districts in the Trust Territory of the Pacific Islands, which is administered by the U.S. Department of Interior through a high commissioner headquartered at Saipan. The other districts are Palau, Yap, Truk, Ponape, and the Mariana Islands.

Rising not more than a few meters above sea level, the Marshalls consist of a double chain of coral atolls about 200 km apart. They have a total land area of about 180 km^2 and a lagoon area of about 11,650 km^2 (Mason, 1951). The chief island is Jaluit; along with several other islands in the Mariana and Caroline groups, it served as a base for Japanese pole-and-line skipjack fisheries prior to World War II. The present district administrative center is on Majuro, which has good accommodations for shipping (Tudor, 1968).

Baiting

Majuro has an irregularly oval lagoon that measures about 45 km long and 17 km wide (Fig. 3). Exploratory cruises of the NMFS 'Townsend Cromwell' had revealed that bait suitable for pole-and-line fishing was abundant at Majuro. Prior to baiting in Majuro Lagoon, we surveyed the lagoon side of the northern islets where schools of silverside, Pranesus pinguis, and sardine, Herklotsichthys punctatus, were reported to be abundant (Hida, 1971). Fair-to-good quantities of both species were seen schooled close to shore in shallow water, some over fairly good seining bottom, and some over rough, uneven bottom of coral sands and rubble interspersed with coral heads.

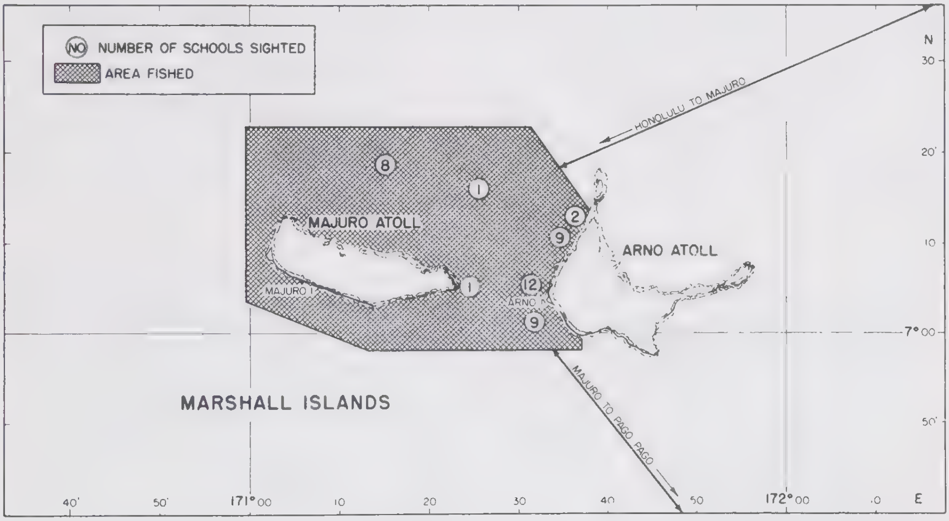


Fig. 3 - Number of schools sighted and the area fished by M/V 'Anela' in the Marshall Islands (February).

On our first stop in the Marshalls, the crew baited twice in Majuro Lagoon and caught 205 buckets of bait in five sets, which required 3.3 hr to complete. One bucket equals 3.2 kg of baitfish. The average catch rates were 62.1 buckets per hour and 41.0 buckets per set; these were far better than those calculated in a June-August 1967 study of Hawaiian skipjack vessels, whose crews averaged only 11.9 buckets per hour and 12.4 buckets per set. A large proportion of the Majuro baitfish was silverside, which ranged from 6.4 to 8.9 cm in total length. Smaller quantities of sardine, taken together with the silverside, ranged from 11.0 to 14.0 cm (T. Hida, personal communication). Underwater observation by an NMFS observer revealed that when the silverside were schooled in the same location as the sardine, the former always concentrated closer to the surface with the latter below.

Silverside and sardine, although considered by the crew to be inferior to the Hawaiian nehu, Stolephorus purpureus, as bait for skipjack fishing, nevertheless were satisfactory as tuna bait. Both species were vigorous in the seine and could be transferred from the seine to the baitwells and "crowded" (concentrated into a small, two-handled push net during chumming) without significant mortalities. Being hardy fish, silverside and sardine could be transported long distances without serious loss. For example, on the 6-day, 2,965-km voyage from the Marshalls to American Samoa, Anela carried about 50 buckets of bait with hardly any mortalities. While being transported, the bait were fed daily on a wet mixture of flaked, boiled skipjack and bread.

Fishing

While in the Marshalls in February, we concentrated our effort in waters immediately adjacent to Majuro and Arno atolls (See map). In 7 days of scouting and fishing, we sighted 42 schools, or an average of 6.0 schools per day. This was slightly better than the Hawaiian vessels' average of 5.4 schools per day in June-August 1967 (Uchida and Sumida, 1971).

Of the 42 schools sighted, we identified 24: 18 skipjack, 3 mixed skipjack-yellowfin Thunnus albacares, 1 mixed skipjack-dolphin, Coryphaena hippurus, 1 rainbow runner, Elagatis bipinnulatus, and 1 mixed rainbow runner-skipjack-yellowfin-kawakawa, Euthynnus affinis. Eighteen schools were unidentified. All schools were found under bird flocks, which varied from 5 to over 1,000 birds. The flocks were composed predominantly of noddy terns, Anous stolidus, although sooty terns, Sterna fuscata, and white terns, Gygis alba, were also quite numerous.

Two large flocks of over 1,000 birds were sighted on the day we arrived in the Marshalls. Anela pursued both schools, which were close to shore along the west coast of Arno. Because we had no bait at the time, we used trolling lines and made several passes through the schools but did not catch any fish.

We experienced several days of good fishing despite the inevitable difficulties of fishing in a new region. Figure 4 shows the crew fishing a good-biting skipjack school in the Marshalls. We pursued and chummed 36 of the 42 schools sighted (86%) and successfully fished 18 (50%) of those chummed. The percentage of schools successfully fished is slightly lower than the 57% success calculated for schools fished in Hawaiian waters (Uchida and Sumida, 1971). We had 2 days when we were unable to catch any fish from the schools fished.

The catch included 3,369 skipjack tuna, 127 yellowfin tuna, 1 kawakawa, 2 rainbow runner, and 1 dolphin. In weight, the catch reached 20.0 M.T. of skipjack and 1.2 M.T. of yellowfin. Catch per day fished (including zero-catch days) was 3.5 M.T. of tuna, slightly higher than the 1967 summer average of 2.8 M.T. calculated for Hawaiian vessels. Ranging from less than 0.1 to 4.4 M.T., catch per school (including zero-catch schools) from 36 schools chummed averaged 0.5 M.T., or half the 1.1 M.T. average of Hawaiian vessels.

By randomly sampling 10 fish from each school fished, we found that the skipjack ranged from 1.6 to 10.6 kg and averaged 5.6 kg. Our data showed that only about 4% of the skipjack landed were less than 4.5 kg. The yellowfin ranged from 5.6 to 13.6 kg and averaged 8.2 kg.

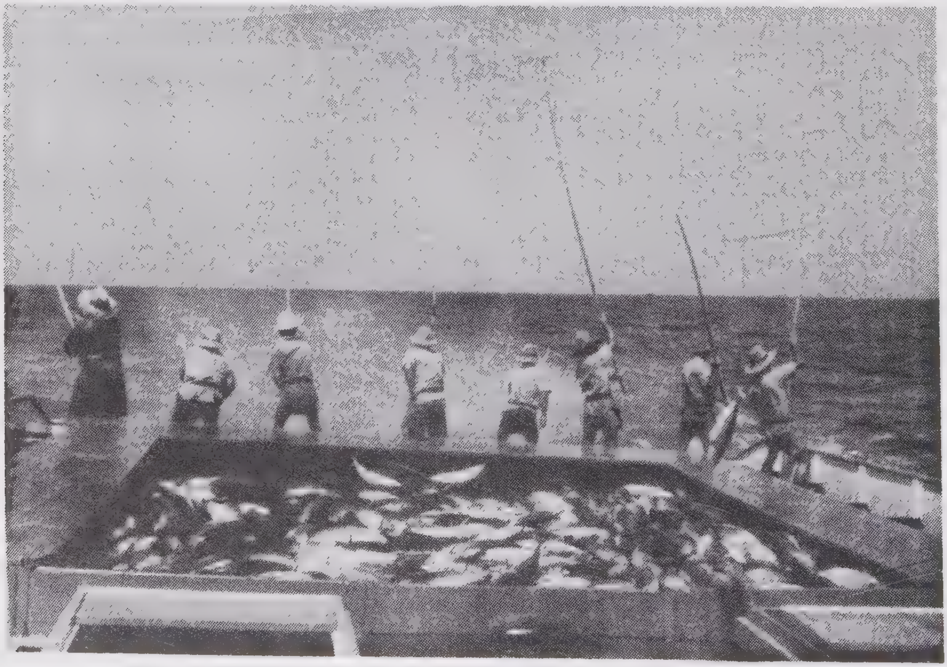


Fig. 4 - The crew of 'Anela' fishing a skipjack school in the Marshalls.

The catch per hook-minute, used here as a measure of the average rate at which fish were caught per hook per minute, ranged from 0.2 to 3.9 fish per hook-minute and averaged 1.1 fish per hook-minute.

Most schools pursued in the Marshalls were "subsurface," where no visible signs of surface movement were detected. We classified the schools as 20 "subsurface," 6 "jumping, " and 1 "boiler"(Scott, 1969). Of particular interest was the "boiler" sighted on February 20. When sighted from a distance, the bird flock of over 1,000 was "working" over what appeared to be breakers (Fig. 5). As it turned out, the "boiling" white water was due to hundreds of fish actively pursuing and feeding on prey at the surface. We made 24 passes through this mixed skipjack-yellowfin school. Seven passes produced no fish. From the remaining 17 passes, the catch varied from 1 to 62 fish. The reason for the small catch on each pass from this large school was that the fish responded to chumming at the stern only for short periods (1 to 11 minutes), then broke off and headed in another direction. The stomach contents of several landed fish, and the regurgitated material on deck, showed that the tuna were feeding on a small anchovy that closely resembled the Hawaiian nehu.

Environmental Conditions

In February, we had reasonably good weather in the Marshalls. The prevailing northeast trades, estimated from sea conditions to be blowing from 18 to 36 km/hr, were sufficiently strong most of the time to raise whitecaps on the blue water outside the lagoon. High winds and rough seas were responsible for the cancellation of only 2 days of fishing. Showers were frequent but brief and did not seriously hinder baiting or fishing.

From expendable bathythermograph (XBT) casts down to 400 m, we obtained data to construct frequency distributions of surface and subsurface temperatures at 100-m intervals (Fig. 6). Surface temperatures around Majuro and Arno were relatively warm with a narrow range from 27.5° to 28.5° C. At 100 m, the temperatures had a relatively wide range--from 21.3° to 27.0° C; but below that, they varied only slightly--ranges from 11.3° to 13.0° C at 200 m, 9.4° to 9.8° C at 300 m, and 8.6° to 8.9° at 400 m. The thermocline was distinct and occurred between 60 and 102 m.

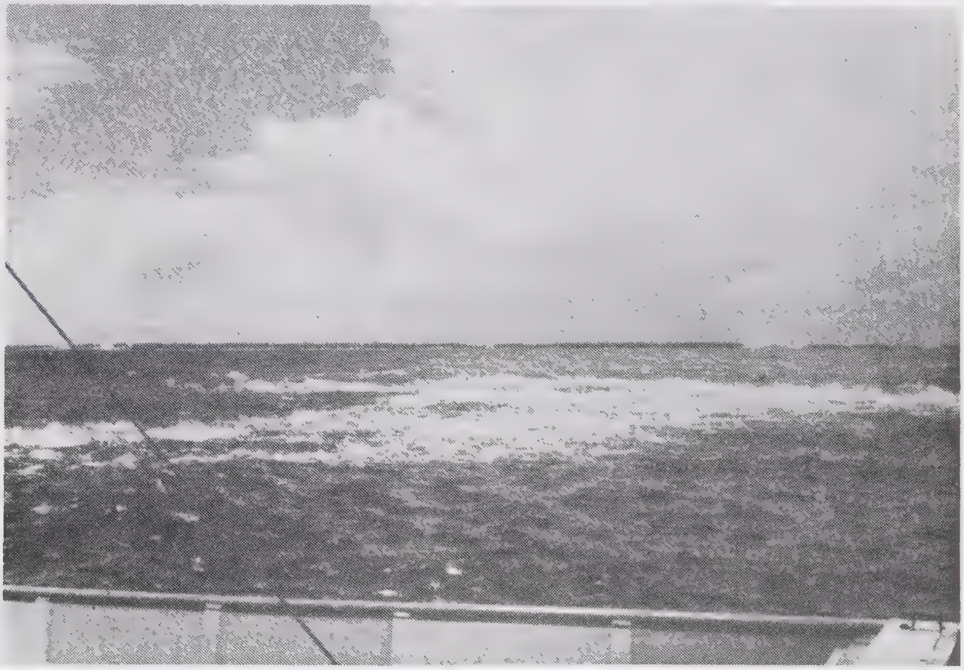


Fig. 5 - A "boiler" school fished off Majuro atoll on February 20, 1972 by the crew of 'Anela.'

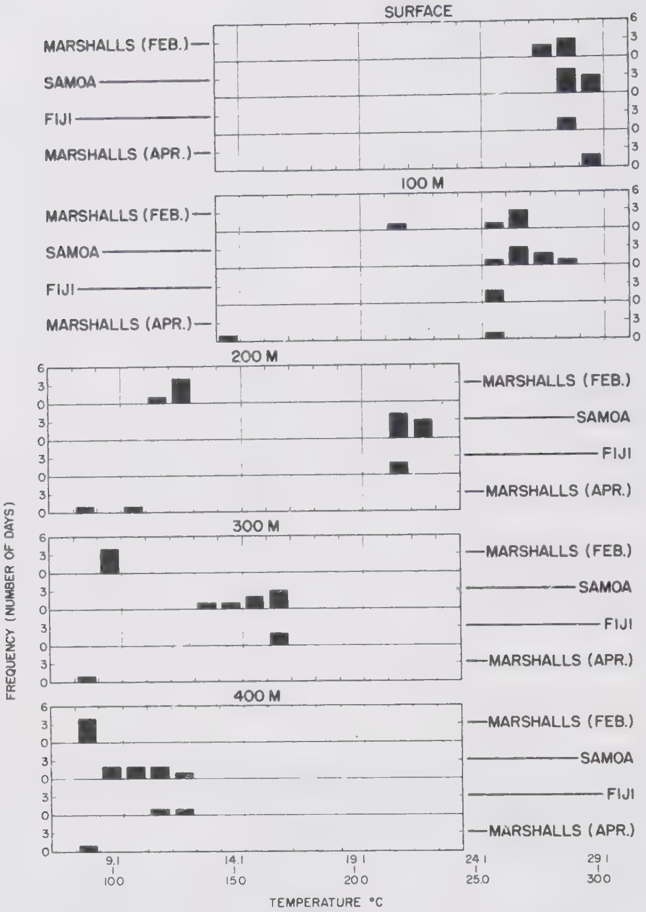


Fig. 6 - Frequency distribution of surface and subsurface temperatures of waters around Marshall Islands (February and April), Samoa, and Fiji, 'Anela' charter cruise, February 8-May 9, 1972.

SAMOA AND FIJI (MARCH 6-APRIL 15)

Anela left the Marshalls on February 29 and arrived at Pago Pago, American Samoa, on March 6. The trip was uneventful except for 1 day of fishing 74 km north-northeast of Apia, Western Samoa, on March 5.

American and Western Samoa are situated between lat 13° and 15° S and extend in an east-west direction from about long 168° to 173° W. They are volcanic in origin (Fig. 7). American Samoa comprises all the islands lying east of long 171° W and is administered by the United States. Pago Pago, on Tutuila, is the principal town and the harbor serves as a port of landing for foreign longline fishing vessels which supply the two American canneries with large, deep-swimming tunas. Western Samoa is a self-governing nation of the British Commonwealth. It has two large, main islands--Upolu and Savaii. The chief town and administrative center is Apia on Upolu.

Lying 925 km southwest of Samoa is Fiji. It comprises 320 islands of various sizes between lat 15° and 22° S and long 177° W and 175° E (Fig. 8). Two of the largest are Vanua Levu and Viti Levu, on which Suva, present capital, is located. Levuka, the former capital on Ovalau, serves as a port of landing for foreign longline fishing vessels. These unload frozen tuna for transshipment to canneries in the United States and Japan.

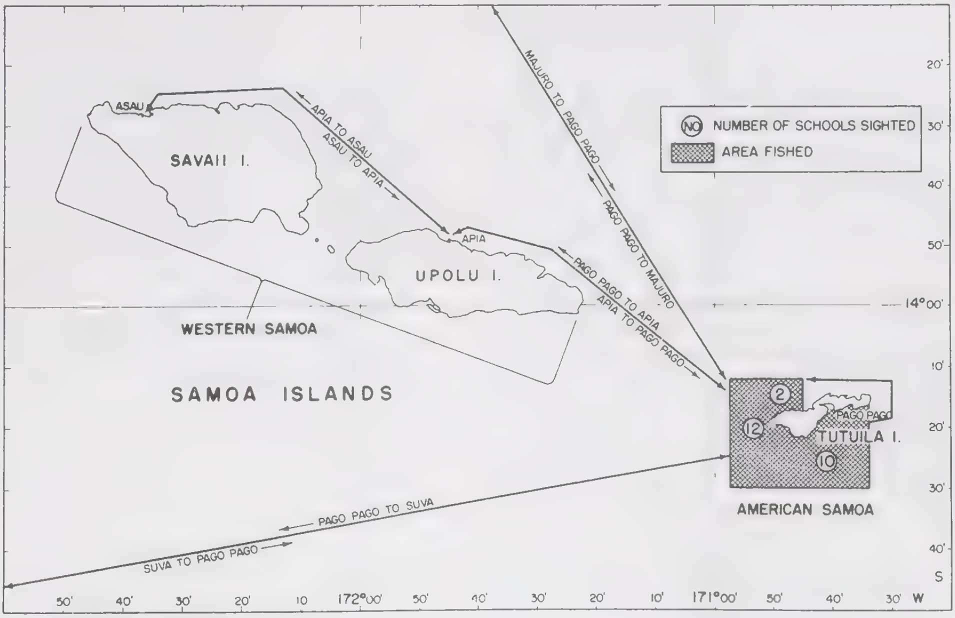
Baiting

American Samoa--Previous bait surveys by the NMFS 'Charles H. Gilbert' indicated that bait might be scarce in both American and Western Samoa (Hida, 1970). We spent 3 days looking for bait in American Samoa. We scouted from shore along the beaches of Pala Lagoon and Fagaitua Bay on Tutuila, and from the skiff along the perimeter of Pago Pago Harbor. We saw small schools of juvenile bigeye scad, Trachurops crumenophthalmus, along the beaches and sardine, jack, Caranx sp., and mullet, Mugil sp., in the harbor, but nowhere did we see baitfish in any quantity. We tried fishing with a 100-w light at night, but the amount of juvenile jack and bigeye scad that congregated around the light was hardly sufficient for tuna fishing by a vessel of Anela's size. We also attempted to scout Aoa, Masefau, Afono, Vatia, and Fagasa Bays, but rough seas prevented Anela from launching the skiff. Bait could not be found in American Samoa, so we decided to attempt baiting in Western Samoa.

Western Samoa--On March 10, we departed Pago Pago Harbor and arrived at Apia Harbor (Fig.7). We scouted intensively along harbor's perimeter and along northwestern shore near harbor's entrance. With exception of a small school of round herring, Spratelloides delicatulus, there were no other baitfish in appreciable quantity. Then we traveled to Asau Harbor on the northern coast of Savaii. There the crew scouted the harbor's perimeter without finding any bait. A night light was also set in an attempt to attract anchovy, which were reported to be in the harbor at times. Again, with the exception of a few jack and bigeye scad, we failed to attract any appreciable quantities of baitfish. Palauli Bay on the southern coast of Savaii also was suggested as a possible baiting ground. But the bay was very shallow and there was no assurance that bait could be found there, so we returned to Pago Pago on March 13. We arranged to depart for Fiji to catch bait. The lack of bait in Samoan waters was in marked contrast to the abundance of bait in Majuro Lagoon.

Fiji--The charter did not include operations near Fiji. However, because bait was lacking in Samoa, we obtained permission from the Government of Fiji to bait in Fijian waters; in return, we agreed to conduct a survey of tuna schools around Fiji. We departed Pago Pago on March 16 and arrived in Suva on March 20.

Runoff from a recent heavy rain had muddied much of the water in baiting grounds near Suva. Therefore, we traveled to Kia Island



ASAU
SAVAII I.
APIA TO ASAU
ASAU TO APIA
MAJURO TO PAGO PAGO
PAGO PAGO TO MAJURO
NO NUMBER OF SCHOOLS SIGHTED
▨ AREA FISHED
APIA
UPOLU I.
PAGO PAGO TO APIA
APIA TO PAGO PAGO
WESTERN SAMOA
SAMOA ISLANDS
2
12
10
PAGO PAGO
TUTUILA I.
AMERICAN SAMOA
PAGO PAGO TO SUVA
SUVA TO PAGO PAGO
20'
30'
40'
50'
14°00'
10'
20'
30'
40'
S
50'
40'
30'
20'
10
172°00'
50'
40'
30'
20'
10'
171°00'
50'
40'
30'
W

Fig. 7 - Number of schools sighted and the area fished by M/V 'Anela' in American and Western Samoa.

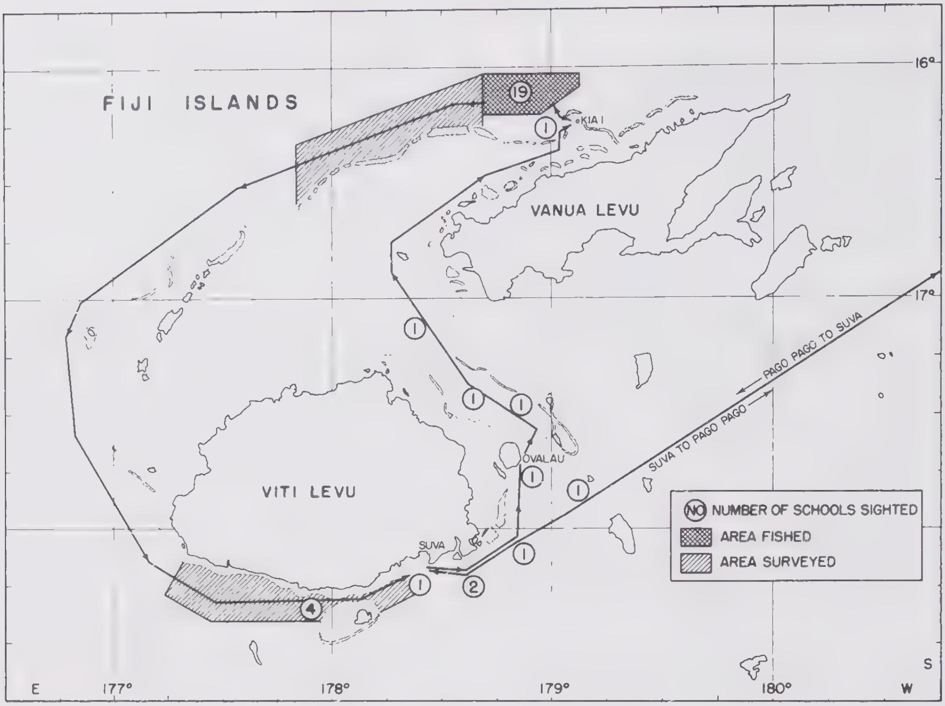


Fig. 8 - Number of schools sighted, area fished, and area surveyed by M/V 'Anela' in Fiji.

north of Vanua Levu and arrived there March 23 (Fig. 8). We surveyed the shoreline and it was immediately obvious that bait was plentiful. We saw bait schooled over rough bottom of jagged rocks and corals, and some over fairly smooth bottom near small, sandy beaches. In the first of two baiting operations, the crew made one set and caught 159 buckets of sardine. After fishing with this bait north of Kia the following day, we returned to the baiting ground. In two sets we caught an additional 110 buckets of sardine and silverside. Sixty buckets were transferred to the baitwells and the remainder released. The crew spent 1.7 hr to catch 269 buckets of bait, an impressive average of 158.2 buckets per hour and 89.7 buckets per set. These were more than double the catch rates calculated for baiting in the Marshalls in February. About 75% of the Kia bait were sardine ranging from 7.6 to 10.2 cm. The smaller silverside were 6.4 to 8.9 cm.

Fishing

American Samoa--Actual fishing time, only 3 days in Samoan waters, was severely limited by the more pressing need to travel between various baiting sites and by unavoidable delays ashore. We fished near Samoa 2 days with bait caught in the Marshalls.

In 4 days of Samoan scouting, we sighted 25 schools, or an average of 6.2 schools per day. Twenty-three schools were sighted as a result of direct scouting for tuna schools. The remaining two, both skipjack, were sighted north of Tutuila after baiting in the north shore bays was cancelled because of rough seas. Anela trolled through both schools but failed to get a strike.

We identified 16 schools as skipjack and 1 as kawakawa; the remainder was unidentified. Bird flocks over the tuna schools in Samoan waters were usually smaller than those found over tuna schools in the Marshalls. A large proportion of the bird flocks was composed of sooty and noddy terns, but white terns, boobies, and shearwaters also were quite common. Of the 25 schools seen, 21 (84%) were pursued and chummed, but only 8 (38%) of those chummed were successfully fished.

The total catch reached 2,407 skipjack weighing 12.1 M.T. and 33 kawakawa. Catch per day fished averaged 4.0 M.T., slightly higher than that calculated for fishing in the Marshalls. Catch per school ranged from 0.2 to 3.7 M.T. and averaged 0.5 M.T. About half the Samoan schools were "subsurface"; the remainder was "jumping".

Compared with Marshalls skipjack, Samoan were usually smaller; about half (56%) were under 4.5 kg. Samoan skipjack ranged from 2.3 to 11.6 kg and averaged 5.3 kg.

The catch rates of schools fished in Samoa did not vary as widely as those calculated for schools fished in the Marshalls in February. They ranged from 0.2 to 2.0 fish per hook-minute, and averaged 0.9 fish per hook-minute. This was slightly below February average in the Marshalls.

Fiji--Tuna schools were numerous in Fijian waters. We sighted 3 schools en route to Suva, 8 schools en route to baiting ground at Kia Island, 19 schools in 2 days of fishing north of Kia, 4 schools at Mbengga Passage while returning to Suva, and 2 schools immediately after departing Suva for Pago Pago. Seventeen schools were identified as skipjack, the remainder unidentified.

Most flocks sighted in Fiji were large: 56% were composed of an estimated 101-500 birds. Noddy terns predominated in all flocks, although shearwaters and tropic birds were common in some flocks.

We sighted a daily average of 5.1 schools during scouting and fishing in Fiji. Eighteen (50%) of the schools sighted were pursued, and 16 (84%) of those pursued were chummed. Twelve schools, or 75%, of those chummed yielded fish, a percentage of success much higher than that calculated for schools fished in Hawaii, the Marshalls, and Samoa. The catch reached 6,227 skipjack, or 19.1 M.T., with catch per day fished averaging an impressive 9.6 M.T. This was more than twice the average catch per day in Samoa. Catch per school ranged from less than 0.1 to 3.8 M.T. and averaged 1.1 M.T. This was identical with that calculated for Hawaiian vessels--but twice the average catch from schools fished in the Marshalls and Samoa.

Ranging from 1.2 to 4.5 kg, and averaging only 2.9 kg, the skipjack caught near Fiji were considerably smaller than the fish caught in the Marshalls and Samoa. The small size was offset, in part, by high catch rates. These varied from 0.1 to 4.4 fish per hook-minute, and averaged 2.3 fish per hook-minute. We obtained good tonnages from most schools fished.

Environmental Conditions

In Samoan waters, Anela found reasonably good weather. Only one baiting attempt and 1 day's fishing were cancelled because of high winds and rough seas. The prevailing east or southeast winds blew at estimated speeds of 18 to 36 km per hour. Showers were frequent and varied from light to heavy, but these did not seriously hinder baiting or fishing. Around Fiji, the winds were either easterly or westerly, and blew from 9 to 28 km per hour. Frequent showers also were a feature of Fiji.

The surface temperatures around Samoa and Fiji were usually warmer than around the Marshalls; they ranged from 28.4° to 29.4° C. Expendable bathythermograph casts showed that the thermocline in the Samoa-Fiji area was rather indistinct; it varied from 43 to 96 m. At 100 m., the temperatures ranged from 27.5° to 28.5° C. At 200 m and below, the temperatures were considerable warmer than at similar depths around the Marshalls. They ranged from 21.2° to 22.8° C at 200 m, 14.0° to 17.0° C at 300 m, and 9.3° to 12.2° C at 400 m (Fig. 7).

MARSHALL ISLANDS (APRIL 23-MAY 2)

On the homeward leg, Anela retraced her path to the Marshalls. It departed Pago Pago on April 16 and arrived in Majuro on April 23 (Fig. 9). We felt it desirable to explore atolls other than Majuro and Arno for concentrations of tuna. We centered our efforts around Jaluit atoll and Kili Island and shifted to Majuro and Arno atolls before returning to Honolulu.

Baiting

Fishing rights in the Marshalls are controlled by local municipalities, the basic units of government on each island or atoll. Before proceeding to Jaluit to bait, we obtained permission from the district administrator in Majuro, who arranged for Anela to bait in Jaluit. Jaluit Lagoon is more than twice the size of Majuro Lagoon; it is 56 km long and 22 km wide (Fig. 9). After fishing near Jaluit and Kili, we returned to Majuro Lagoon to catch bait. Unlike February's baiting con-

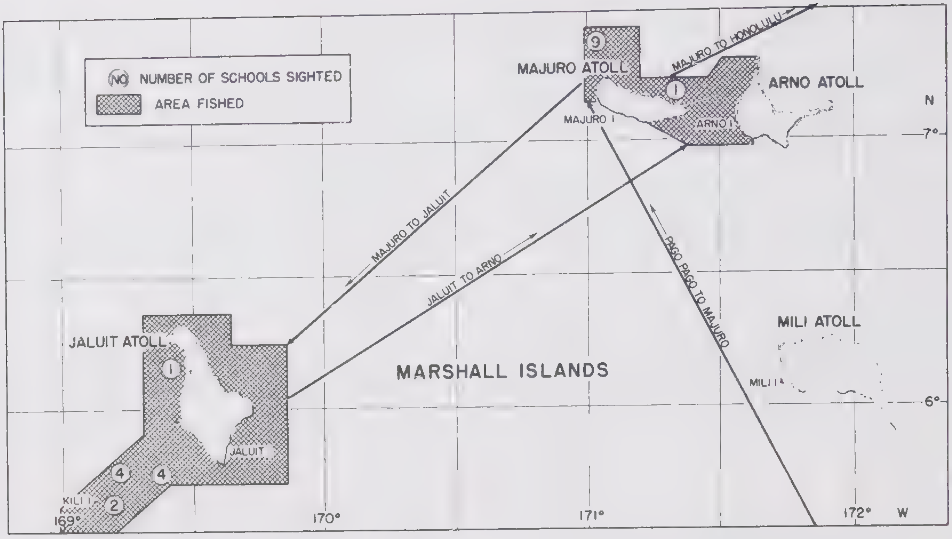


Fig. 9 - Number of schools sighted and area fished by M/V 'Anela' in the Marshall Islands (April).

ditions, we saw none along the shoreline. High winds and rain made visual scouting from the skiff extremely difficult and were partly responsible for our failure to see baitfish schools.

Overall, baiting at Jaluit and Majuro required 3.6 hr. In two sets in Jaluit Lagoon, the catch totaled 189 buckets, an average of 94.5 buckets per set. Catch per hour, which includes the Majuro effort, was 52.5 buckets. After filling baitwells, about 30 buckets of bait remaining in the seine were released. The catch was made on the lagoon side of the shoreline of Emidji island over relatively smooth sand bottom; it consisted almost entirely of sardine ranging from about 8.9 to 11.4 cm long.

Fishing

In April, Anela found Marshalls' conditions considerably changed. Perhaps most significant was size of bird flocks. In February, nearly half the flocks had more than 500 birds; in April, all flocks had 500 birds or fewer. However, there was no change in species composition: predominantly noddy terns, with few sooty and white terns. School sightings in April totaled 23 schools in 4 days, or an average of 5.8 schools per day. Of these, seven were skipjack, eight yellowfin, one mixed skipjack-yellowfin, and seven unidentified.

Ten of the schools sighted were pursued and chummed. Of these, only three (30%) were successfully fished, a rate considerably below February's. There were 3 zero-catch days in 4 days of fishing.

The crew caught 300 fish totaling 2.0 M.T. from two schools of skipjack. One school of yellowfin yielded 44 fish, which weighed 0.6 M.T. The catch per day was very low, averaging only 0.6 M.T., or about one-sixth average catch per day in February. Catch per school was similarly low; it ranged from 0.6 to 1.0 M.T. and averaged only 0.3 M.T.

Although a large proportion of schools pursued in February was "subsurface," the majority of schools pursued in April were "jumping." We had seven "jumping" schools, two "subsurface," and one "finning".

The size of skipjack caught in April did not vary as widely as in February. The April fish were medium-sized--between 5.9 and 7.5 kg and averaging 6.7 kg. For the one yellowfin school fished, the size range was 12.2 to 18.0 kg and the average 14.4 kg; this was considerably larger than February's average size of yellowfin. The catch rates calculated for the three schools fished in April varied between 0.3 and 0.5 fish per hook-minute, and averaged only 0.4 fish per hook-minute. The figure was less than half the catch rate of the February schools.

Environmental Conditions

On homeward leg, changes were evident in environmental conditions. Our weather observations showed that in April the northeast trades had diminished, and the winds had shifted to the east and southeast. The weather was exceptionally mild. Wind speeds were estimated at 9 to 28 km per hour but more frequently at lower speeds.

Surface temperatures, which ranged between 27.5° and 28.5° C in February, were slightly higher at 29.1° and 29.2° C in April. Very noticeable changes had occurred in subsurface layers, particularly in the depth to the top of the thermocline and in the temperature at 200 m (Fig. 6).

CONCLUSIONS

We believe that a commercial pole-and-line fishery for surface schooling skipjack and yellowfin tuna could become a reality and a source of revenue in the Marshall Islands. Not only were the potentials of the skipjack tuna resources impressive, but so were the potentials of the bait resource. The seasonal availability of tuna schools is not yet clearly understood and further studies are necessary. Likewise, stocks of sardine and silverside in the Marshalls need to be studied to determine how well they will withstand fishing pressure by commercial pole-and-line vessels.

Concerning American Samoa, we believe that it is premature to reach conclusions regarding a pole-and-line fishery there. Our limited observations and a previous NMFS survey of Samoan waters have shown that skipjack are present in sufficient quantities to support a commercial fishery at least large enough to meet all local demands. A vital prerequisite is the means of catching the tuna. Bait is scarce, but its seasonal distribution and abundance should be studied further.

We can conclude, tentatively, from our short stop in Fiji that skipjack schools, sighted at rate of 9.5 schools per day north of Kia Island, occur in sufficient numbers to support a small commercial fishery. But the short survey precludes conclusions about the abundance in other areas or in other times of the year in Fiji. Bait appears plentiful. From our observations and conversations with Fijian government observers, it is evident that many species of bait occur around the numerous islands of the Fiji group, and that day and night baiting are possible.

Tuna schools were found relatively close to all island groups surveyed. So a profitable tuna fishery in the Marshalls, Samoa, and Fiji could be based on small vessels of limited bait capacity and cruising range, such as those in Hawaiian waters. Shoreside support facilities for servicing the vessels and processing the catch are already well established in American Samoa and Fiji. Both service foreign longline vessels. The Marshalls, however, lack all such facilities.

ACKNOWLEDGMENTS

Many people worked hard to make this cruise a success. We thank Captain George K. Higashide and his crew for helping us adjust to life on a commercial fishing vessel and for contributing time and effort to help us collect data; Mr. Frank Goto of the United Fishing Agency and Mr. Jack Shinsato of Angel Fishing Company for providing administrative and logistical support; Senator Amata Kabua, President of the Congress of Micronesia, and Oscar de Brum, District Administrator, and their staffs in the Marshalls; Dr. Stanley Swerdloff, Director of the Office of Marine Resources, and his staff in American Samoa; the Government of Western Samoa, Mr. William Travis, Fisheries Officer of the Department of Agriculture, Forests, and Fisheries, and his staff; the Government of Fiji, Mr. B. Vunibobo, Secretary for Ministry of Agriculture, Forestry, and Fisheries; and Mr. Robert E.K.D. Lee, Manager of the FAO Local Tuna Project, and his staff.

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TARACTES RUBESCENS AND *TARACTICHTHYS STEINDACHNERI* FROM HAWAIIAN WATERS

The various species of the family Bramidae are mostly high-seas fishes with the possible exception of *Eumegistus.* Although capture records of adult *Taractes rubescens* (Jordan and Evermann, 1887) and *Taractichthys steindachneri* (Döderlein, 1883) are few, Mead (1972) surmises that they are probably widespread in the tropical oceanic Pacific. Most of the documented accounts of the occurrence of these two species in the Pacific Ocean are of juvenile stages taken from stomachs of large predators. In the Pacific, *Taractes rubescens* has been recorded from a few widely separated localities between lat. 05°48′N and 02°26′S and long. 88°46′ and 155°W. All except one of the documented captures are of juveniles smaller than 120 mm. The only adult specimen was taken by a Japanese longliner at lat. 05°48′N, long. 126°00′W. *Taractichthys steindachneri* is also known mostly from juveniles. They have been captured at widely separated localities between lat. 40°48′N and 04°46′S and long. 165°35′W and 98°28′E. Although adult specimens of this species are also taken incidentally by Japanese longliners, documented capture localities are available in the Pacific for only four specimens. This note records the capture of the adults of 10 *Taractes rubescens* and 2 *Taractichthys steindachneri* from Hawaii and also provides some observations on the ecology of the two species.

Within the area around the Hawaiian Islands bounded by lat. 10°-30°N and long. 150°-170°W, *Taractes rubescens* was previously known from one juvenile measuring 27.5 mm in standard length (SL) and *Taractichthys steindachneri* was known from three juveniles measuring 17.0, 42.5, and 130.0 mm SL (Mead, 1972). The latter species was also known from an adult specimen (*Taractes longipinnis* = *Taractichthys steindachneri*) "about 2 feet long" (Gosline and Brock, 1960). However, *T. steindachneri* is probably more common than indicated: Mead (1972) cites a personal communication from W. A. Gosline (December 1963) in which it is indicated that fishermen in Hawaii are familiar with this species. The 12 bramids reported here were captured on longline gear at nine fishing stations during cruise 101 of the NOAA vessel *Charles H. Gilbert* between 17 May and 6 June 1967 (Table 1). The fishing stations were from 14 to 30 km off the coast of Waianae, Oahu, over depths of 1,800-3,000 m. The surface water temperature ranged from 25.5° to 27.4°C and the salinity from 34.5‰ to 34.9‰ at the fishing stations. Other fishes caught together with the bramids, in order of abundance, were *Alepisaurus* sp., *Prionace glauca, Thunnus obesus, Tetrapturus audax, Xiphias gladius, Alopias* sp., *Gempylus serpens, Katsuwonus pelamis, Acanthocybium solandri, Thunnus albacares, Tetrapturus angustirostris,* and *Isurus* sp.

Three of the *Taractes rubescens* and both of the *Taractichthys steindachneri* were frozen after capture. Approximately 5 yr later, body measurements and counts on two *Taractes rubescens* and two *Taractichthys steindachneri* were made in the laboratory after the specimens thawed out (Table 2). The five preserved specimens are presently in the Southwest Fisheries Center, Honolulu Laboratory's fish collection.

TABLE 1.—Capture locality of *Taractes rubescens* and *Taractichthys steindachneri*.

Date 1967	Position		*Taractes rubescens*			*Taractichthys steindachneri*		
	Lat. N	Long. W	Number	Length	Sex[1]	Number	Length	Sex[1]
				mm			*mm*	
18 May	21°26′	158°22′	1	729	M	—	—	—
19 May	21°34′	158°34′	1	749	M	—	—	—
20 May	21°19′	158°22′	2	781	M	1	611	F
				635	F			
21 May	21°23′	158°24′	2	522	F	—	—	—
				662	F			
22 May	21°16′	158°15′	1	713	M		—	
26 May	21°17′	158°17′	1	730	M	—	—	—
28 May	21°16′	158°16′	1	[2]—	[2]—	—	—	—
3 June	21°21′	158°18′	—	—	—	1	644	F
6 June	21°20′	158°26′	1	760	M	—	—	—

[1] M = male, F = female.

[2] Not determined.

The primary purpose of cruise 101 of the *Charles H. Gilbert* was to determine if longline catch rates for *X. gladius* around Hawaii could be improved by fishing at night. Also included in the fishing experiment was a comparison of Pacific saury, *Cololabis saira*, and squid, *Loligo opalescens*, as bait, and a comparison of the effect of 9.1-, 18.3-, and 36.6-m float lines on the catch rates. Although the number of specimens taken was small, it was interesting to examine the fishing results as they pertain to the bramids.

During cruise 101 longline fishing operations were conducted in two general areas: one off the coast of Hilo, Hawaii, and the other, as noted earlier, off the coast of Waianae, Oahu. The 3 days of fishing off Hilo did not produce any bramids. Off Waianae, bramids were taken on 9 of the 19 days fished in that area. Although the data are too few to make definitive conclusions, it is of interest that slight environmental differences existed in the two areas, which may in part account for the fact that no bramids were taken off Hilo. The surface water temperature was slightly cooler off Hilo, ranging from 24.7° to 25°C as compared with 25.5° to 27.4°C off Waianae. The salinity of the water at the surface ranged from 34.4‰ to 34.6‰ off Hilo and 34.4‰ to 34.9‰ off Waianae.

As far as I know, *Taractichthys steindachneri* and *Taractes rubescens* are not commonly caught by the Hawaiian longline fishermen. This may be because longlines are usually set and retreived during daylight hours. The fact that they were taken on cruise 101 of the *Charles H. Gilbert* when the longlines were fished at night suggests that they may be nocturnal feeders. The results of the experimental use of the float lines of different lengths suggest that they may also be subsurface feeders: More were taken when the longline gear fished deeper, i.e., had longer float lines. Considering only the stations off the Waianae coast, 2,340

TABLE 2.—Measurements and counts on two specimens of *Taractes rubescens* and two specimens of *Taractichthys steindachneri*.

Measurements and counts	*Taractes rubescens*		*Taractichthys steindachneri*	
Standard length (mm)	660	663	538	568
Measurements (in percent of standard length)				
Head length	31.8	32.3	29.2	30.8
Depth of body at origin of dorsal fin	40.0	40.3	45.7	48.9
Least depth of caudal peduncle	7.7	7.5	6.5	7.2
Horizontal diameter of eye	6.4	6.6	6.3	6.5
Snout to origin of dorsal fin	38.6	39.5	36.0	41.9
Snout to origin of anal fin	62.7	60.5	51.1	51.6
Snout to origin of pectoral fin	32.6	31.7	29.4	31.7
Length of pectoral fin	42.7	43.4	42.4	42.1
Length of ventral fin	[1]—	15.2	7.4	8.4
Length of longest dorsal ray	34.1	32.1	38.8	[1]—
Length of longest anal ray	28.8	27.3	30.5	37.8
Counts:				
Dorsal fin	30	30	35	35
Anal fin	20	20	29	28
Pectoral fin	21	20	20	20
Gill rakers	2+8	2+8	4+7	2+8
Scales in horizontal series	[2]45	[2]47	37	37

[1] Damaged.

[2] Excluding the enlarged keel scales.

hooks were fished on longline baskets with 9.1-m float lines, 2,160 hooks on baskets with 18.3-m float lines, and 2,340 hooks on baskets with 36.6-m float lines. No specimens were taken on longline gear with 9.1-m float lines. One *Taractichthys steindachneri* and seven *Taractes rubescens* were taken on longline gear with 18.3-m float lines. One *Taractichthys steindachneri* and three *Taractes rubescens* were taken on longline gear with 36.6-m float lines.

Saury and squid were used as bait on alternate baskets on each fishing station. More bramids were taken on hooks baited with saury than with squid. Nine *Taractes rubescens* were caught on hooks baited with saury, and two on hooks baited with squid. Both of the *Taractichthys steindachneri* were caught on hooks baited with saury. These results would indicate that fish constitute an important part of the diet of these bramids. However, only one of five stomachs (4 *Taractes rubescens* and 1 *Taractichthys steindachneri*) had fish remains. Squid and shrimp remains were more frequent in the stomachs.

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A NON-PARAMETRIC APPROACH TO THE ESTIMATION OF RELATIVE CHANGE IN FISH POPULATION SIZE FROM EGG AND LARVAL SURVEYS

By

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INTRODUCTION

Biological surveys in the ocean are, most often, carried out for two purposes; to locate and estimate the abundance of organisms. This requires sampling and the subsequent processing of the data. Classical theory prescribes how both should be done to insure accuracy and reliability, but rarely, if ever, can these rules be strictly adhered to in surveys at sea. Such surveys are expensive in terms of money and manpower, and one is seldom granted the luxury of tailoring a survey to one's own interests. Compromises are made and what results is a mélange of good and bad, of acceptable and unacceptable procedures in the collection of the samples and in the data analysis and one can hope for little more without massive increases in expenditures for survey work. The analysis of data from such surveys is subjective and often open to question, and their value can be determined only when independent data are available for confirmation. In this paper, estimates of trend in the size of the spawning population of the Pacific sardine (*Sardinops caerulea*) based only on the number of eggs per station collected on the extensive surveys of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) conducted from 1951 through 1960 are compared to similar estimates from both catch data and the much more complete analysis of Murphy (1966).

ANALYSIS OF SURVEY DATA

Whenever it is necessary to utilize sampling techniques to draw conclusions about some larger population, several fundamental decisions must be made. These decisions range from the determination of a basic sampling scheme to the analysis or summarization to be carried out on the data. Perhaps the most basic question to be asked is whether the process can incorporate theoretical sampling designs and statistical techniques or whether it is a process of data collection and analysis based largely upon intuition, judgement, and ingenuity. The present trend in the scientific community is to overrate the theoretical and underrate the practical techniques of data reduction and evaluation. As stated by Tukey (1963), "We have used our growing ability to mathematize and statisticate the simple to help us to err by denying the reality or relevance of the complex." On the other hand, quantitative ecologists and statisticians dealing with natural and transient populations have long recognized the inherent limitations of classical statistical techniques and have relied most heavily on methods requiring only limited theoretical assumptions.

Two issues lie at the heart of the discussion: 1) probability sampling and 2) the normal or Gaussian distribution. In a probability sample all units have a finite and known chance of inclusion in the sample. Thus the frequency distribution of any estimate or function of estimates can readily be derived mathematically or generated by repeated sampling. Non-probability sampling schemes such as judgement, haphazard, accessibility or systematic sampling present no such opportunity for development of a full underlying theory. Their usefulness can usually be examined only when results are available from a complete census or from other sampling schemes.

Many investigators have long realized that assumptions of normality have little validity in the treatment of survey data except for the means of large numbers of observations and that the assumption of this distribution has a marked effect on the associated variances of the estimated parameters. This realization is, in fact, responsible for the scarcity of estimation techniques available in survey work. Alternatively, numerous attempts have been made to describe the distribution of organisms in time and space. The degree of success has, in general, been inversely related to the magnitude of the space-time continuum. Characteristically the zero-class (no organisms per measurement unit) estimated from a specific theoretical distribution is either seriously over- or underestimated. Since a zero sample may either delimit the spatial range or may be due to sampling variability alone, the use of these samples to choose among alternative models is questionable as is the process of combining data where outcomes are rare. Large scale pheno

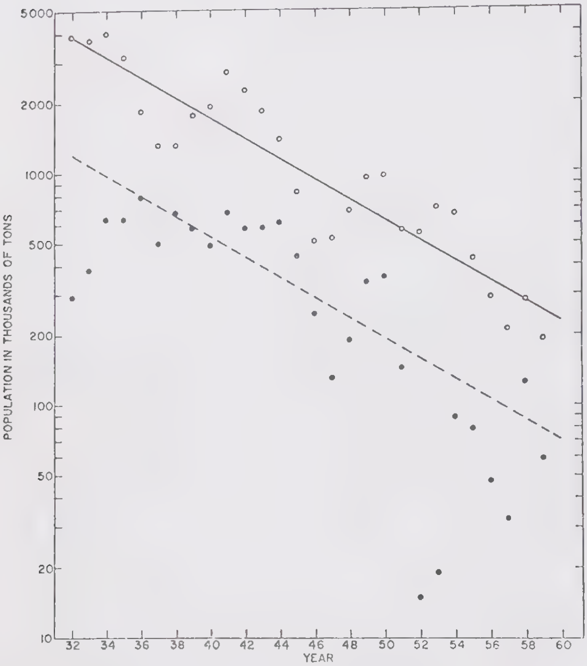


Figure 177. Spawning biomass. • – Murphy's estimates; ∘ – total catch. Lines are the least squares fit for the years 1936–1950.

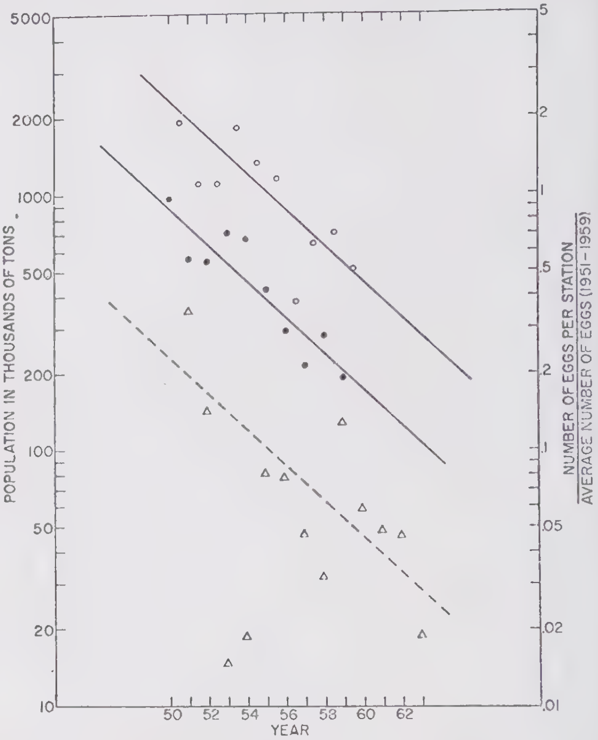


Figure 178. Spawning biomass (1951–1960). • – Murphy's estimates; △ – total catch; ∘ – number of eggs per station estimated for survey data.

menon, or at least sparsely sampled large scale phenomena seem little attuned to the strictures of mathematical or statistical theory.

The general tendency in survey work is 1) to decide upon a sampling unit, 2) to determine a sampling plan and 3) attempt to relate these results to those from similar surveys or to other information available about the population under study. In oceanic survey work the difficulties involved in carrying out the first two steps are enormous. The last seems almost insurmoutable. It is the purpose of this paper to show evidence that simple, admittedly subjective and intuitive, ocean-survey procedures are effective in monitoring relative changes in the spawning population and thus to offer a ray of hope for the effectiveness of similar efforts.

METHODS

A detailed account of the scientific investigation of the Pacific sardine by CalCOFI has been given by Murphy (1966). In particular, his estimates of the total spawning population were calculated for the years 1932–1959. The estimates were based on the records of aged catches and fishing effort and independent estimates of natural mortality, fishing rates and population size. Since the age structure of a population changes constantly, numbers of spawners have little meaning. MacGregor (1957) showed that fecundity is nearly proportional to biomass; hence variations in total biomass will be used here as a basis for comparison.

Murphy's estimates of biomass, plotted in Figure 177, show a logarithmic decline in the spawning population over the period 1932–1959 with quite systematic variations above and below the general trend. The total catch figures, also plotted in the Figure, show a similar decline and in fact the calculated trend lines are nearly identical. Because of the rapid increase in effort prior to 1936 and the rapid decline of vessels due to bankruptcy and diversion to other fisheries after 1950, only data for the period 1936–1950 were used in the calculation of the regression lines. It is evident that the two sets of data depict the same overall trend and quite similar year-to-year variations. Also suggested is a change in the rate of decline about 1950. This corresponds to a doubling of the natural mortality rate assumed by Murphy in his calculations after the 1949 year class. In Figure 178, Murphy's line is recalculated for the period 1951–1959 and extrapolated to the catch data. Again the agreement is good in spite of the apparently great variability of effort encountered during this period.

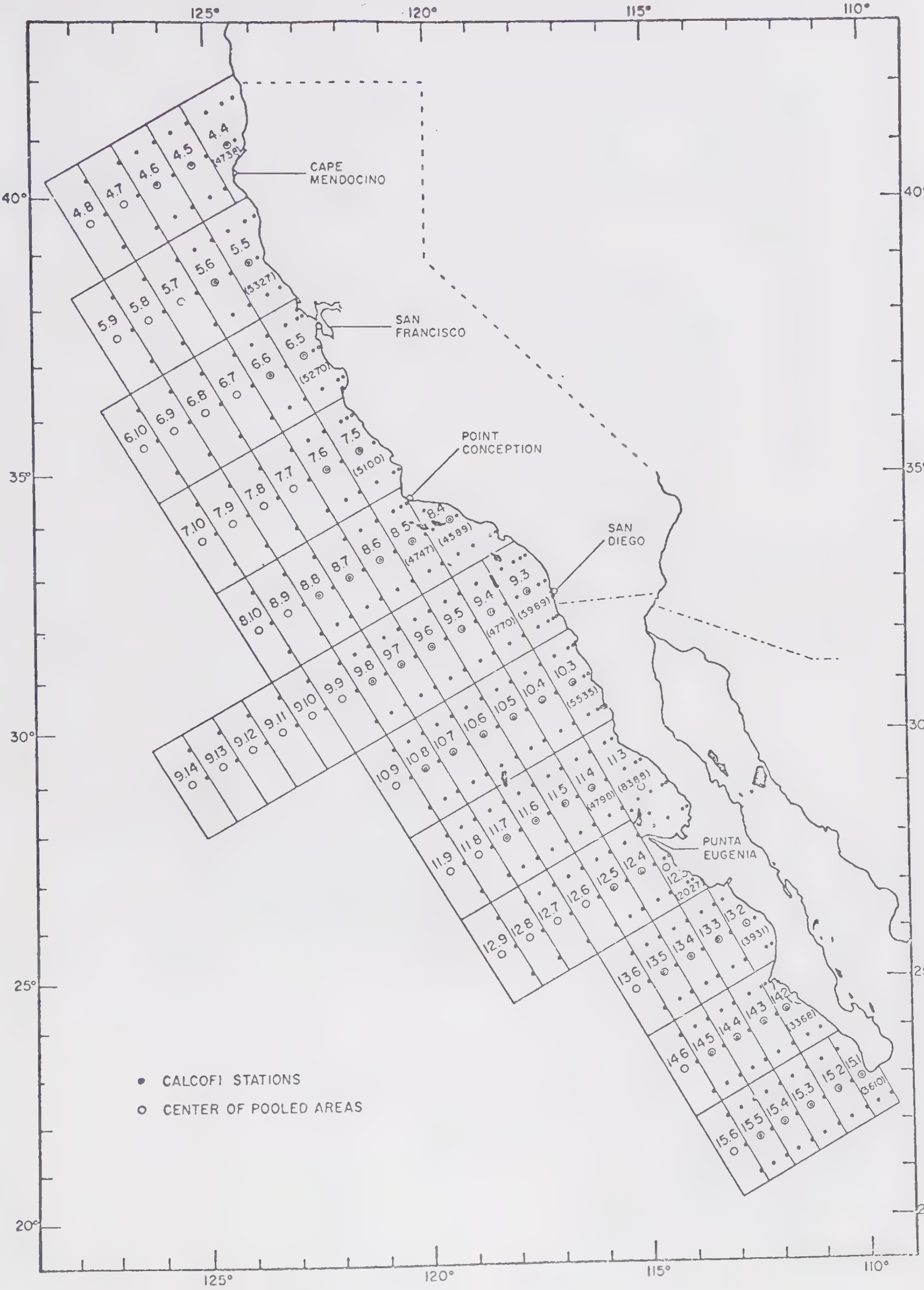
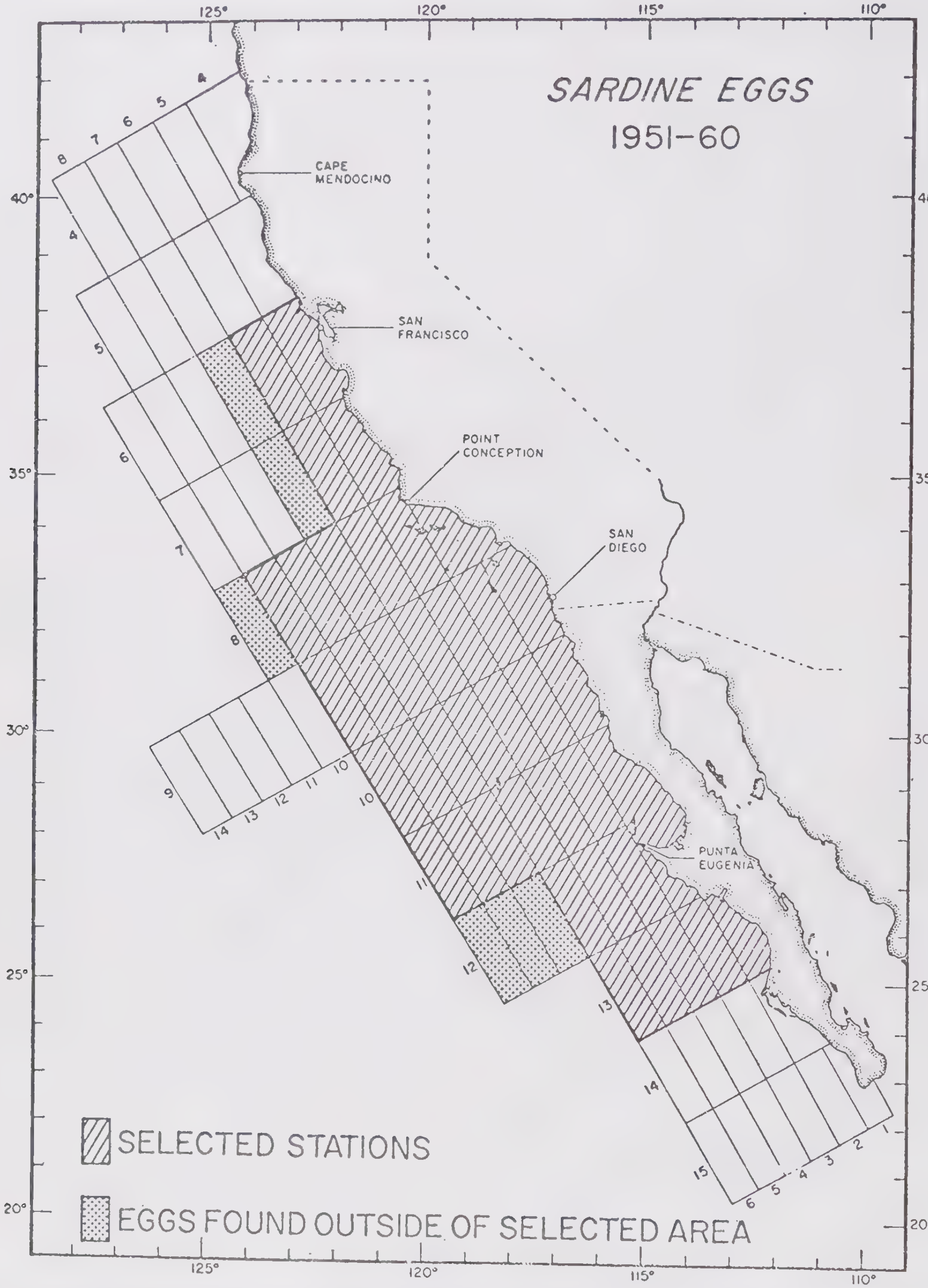

CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
● CALCOFI STATIONS
○ CENTER OF POOLED AREAS
125°
120°
115°
110°
40°
35°
30°
25°
20°

Figure 179. Pooled areas of the CalCOFI survey region.


SARDINE EGGS
1951–60
125°
120°
115°
110°
40°
35°
30°
25°
20°
CAPE MENDOCINO
SAN FRANCISCO
POINT CONCEPTION
SAN DIEGO
PUNTA EUGENIA
4
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SELECTED STATIONS
EGGS FOUND OUTSIDE OF SELECTED AREA

Figure 180. Outlined region shows total area occupied at some time during the period 1950–1960; crosshatched areas were regularly occupied and included in the analysis; dotted areas contained some spawning but were not regularly occupied.

Table 96. Average number of sardine eggs ($\log_{10}$) of positive hauls

Pooled areas[1]	Year									
	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
8–9	1·472	1·100	1·421	1·600	1·543	1·526	2·101	1·678	1·647	1·428
10–11..............	1·736	1·787	2·088	1·669	1·649	1·768	1·599	1·548	1·675	1·554
12–13..............	2·414	1·809	1·708	1·805	1·986	1·967	1·372	·914	·956	2·250

[1] Includes only selected stations, see Figure 180.

Table 97. Percent positive stations

Pooled areas[1]	Year									
	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960
8–9	15·1	9·0	3·0	20·7	16·0	10·0	6·0	24·7	24·6	14·5
10–11..............	29·1	20·0	19·4	44·7	27·1	21·3	8·8	8·2	9·8	10·8
12–13..............	25·5	24·0	23·3	17·4	9·4	12·5	9·2	2·9	4·0	3·6

[1] Includes only selected stations, see Figure 180.

For purposes of this study, Murphy's estimates were assumed to be the best representation of the overall trend as well as year-to-year variations. The question to be answered is whether any reasonable manipulation of the data from egg surveys might substantiate these estimates for the period 1951—1959. Intuitively one would think that changes in the level of spawning would be reflected in either the number of eggs per positive haul (density) shown in Table 96 or in the proportion of positive hauls (coverage) shown in Table 97 or perhaps both. Egg numbers, however, would be expected to vary geometrically for several reasons: 1) the spawning population is undergoing logarithmic changes, 2) favourable or unfavourable environmental factors would be expected to affect the spawned eggs proportionally and 3) the almost universal prevalence in population numbers of geometric or logarithmic changes in abundance (Williams, 1964).

Although spawning occurred over the complete survey pattern of the CalCOFI in the first 7 months of most years, 1951 through 1960, the major centers of spawning activity shifted from south to north in the latter years, 1958 through 1959. Accordingly, in order to include all possible spawning areas, averages were calculated for the entire survey area within each calendar month. The sampling unit used here (Fig. 179) is a pooled area 40 by 120 miles containing from 1 to 6 stations of the CalCOFI pattern with an overall average of four stations per unit. Since some stations or part of the survey region were infrequently occupied over the 10-year period, only regularly occupied stations were included in the analysis (Fig. 180). The sampling procedure for the data used is the standard CalCOFI oblique tow standardized to a unit of 10 square meters of sea surface (Ahlstrom, 1953). Only data for the first 7 months of each year were used because surveys were not consistent in the last five.

RESULTS

Table 98 shows that the mean per positive haul, while showing some trend, remained quite stable during periods of apparent decline and Table 99 reveals that the proportion of positive hauls, in general, varied directly with the mean per haul. In Table 100, the anti-logarithm of the mean per positive haul is multiplied by the proportion of positive hauls to obtain an estimate of the mean per station. These values, expressed as a fraction of the average for the period, are shown in Figure 178 for comparison with Murphy's estimates. The general trend is clearly similar and the year-to-year variation agrees very well if the survey values, reflecting a population in existence from January through July, are considered intermediate between two yearly estimates at about 1. September.

The estimates of the mean per station for each year are the simple averages of the monthly means which are based on a selected group of stations regularly occupied over the period 1951—1960. No attempt was made to correct for variations in sampling pattern within the selected area nor were adjustments made for difference in environmental conditions. The close agreement with other indicators of population trend

Table 98. Average number of sardine eggs ($\log_{10}$) of hauls

Year	Month							Average
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	
1951........	1·864	2·541	1·744	1·705	1·807	1·565	1·862	1·870
1952........	1·530	1·674	1·755	1·925	1·708	1·760	1·629	1·712
1953........	1·462	1·619	1·646	2·241	1·421	1·271	3·218	1·840
1954........	1·303	1·644	1·828	1·602	1·659	1·737	2·030	1·686
1955........	1·989	1·976	1·566	1·383	1·892	1·684	1·565	1·722
1956........	1·643	1·461	1·483	1·538	1·900	1·836	2·584	1·778
1957........	·979	1·830	1·183	2·021	1·926	1·015	2·415	1·610
1958........	1·683	1·937	1·648	1·823	1·484	1·288	1·471	1·619
1959........	1·421	1·536	1·411	1·928	1·985	1·569	1·727	1·654
1960........	1·575	1·962	1·576	1·860	1·449	1·444	1·760	1·661

Table 99. Percent positive stations

Year	Month							Average
	Jan.	Feb.	Mar.	Apr.	May	Jun.	Jul.	
1951	14	12	25	26	28	26	21	21·7
1952	23	16	21	21	19	14	8	17·4
1953	3	21	19	12	16	13	8	13·1
1954	19	27	36	42	35	39	22	31·4
1955	16	20	25	29	23	22	10	20·7
1956	3	18	31	16	19	17	7	15·8
1957	7	6	11	5	10	5	9	7·6
1958	17	13	22	7	12	5	13	12·7
1959	12	23	11	11	8	12	11	12·6
1960	13	11	10	4	4	11	11	9·1

Table 100. Estimated average number ($N\bar{P}$) of sardine eggs per haul

Year	$\overline{\log N}$	N	$\bar{P}$	$N\bar{P}$	$N\bar{P}/\overline{N\bar{P}}$
1951........	1·870	74·1	0·217	16·1	1·96
1952........	1·712	51·5	0·174	9·0	1·10
1953........	1·840	69·2	0·131	9·1	1·11
1954........	1·686	48·5	0·314	15·2	1·85
1955........	1·722	52·7	0·207	10·9	1·33
1956........	1·778	60·0	0·158	9·5	1·16
1957........	1·610	40·7	0·076	3·1	·38
1958........	1·619	41·6	0·127	5·3	·65
1959........	1·654	45·1	0·126	5·7	·70
1960........	1·661	45·8	0·091	4·2	·51

obtained from these estimates shows that such refinements might be used to reduce the inherent variability. In any case, there is convincing evidence that routine sampling (at about 75 to 100 stations per month) over a large spawning area (175 000 square miles) can provide information on relative size of a spawning populations.

SUMMARY

The usefulness of egg and larva surveys for monitoring dynamic fish populations has often been questioned. For many species, the areal coverage required is extensive and thus the sampling density is small. In addition little is known about day to day or area to area sampling variability and standard techniques such as random sampling are rarely feasible. As a result the proper numerical analysis, both of type and extent, of the data is open to question. Some phenomena, however, appear almost universally, such as the inclination to proportional or logarithmic changes in measures of central tendency and variability. By admitting only that spawning levels are basically logarithmic and that these levels will be proportional to some unknown environmental conditions, it was found that for an extensive period (10 years), the average number of eggs per station computed as the anti-logarithm of the mean logarithm per positive haul multiplied by the proportion of positive hauls, when averaged over the total spawning area, reflected the same rate of population decline as evidenced by both the catch data and the estimates obtained by Murphy (1966). Since no distributional assumptions were made, little is known about the associated variability of this estimate. It should be noted that this estimate differs algebraically only slightly from log $(x + 1)$ where the number per positive haul is large.

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